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VOLUME 99, NUMBER 335 DECEMBER 12, 1990

Review of the *Bullia* Group (Gastropoda: Nassariidae) with comments on its Evolution, Biogeography, and Phylogeny

by

Warren D. Allmon

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Bulletins of American Paleontology

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Library of Congress Card Number: 90-63452

The publication costs of this volume were in large part defrayed by a generous grant of $15,000 from the EXXON Corporation. The Paleontological Research Institution gratefully acknowledges this recognition and support of its publications program.

Printed in the United States of America
Allen Press, Inc.
Lawrence, KS 66044 U.S.A.

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REVIEW OF THE *BULLIA* GROUP (GASTROPODA: NASSARIIDAE) WITH COMMENTS ON ITS EVOLUTION, BIOGEOGRAPHY, AND PHYLOGENY

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ABSTRACT

The "*Bullia* group", comprising those gastropods of the family Nassariidae not assignable to the subfamilies Nassariinae or Cylleninae, is a relatively small group presently confined to temperate and subtropical shallow water habitats in the South Atlantic and Indian Oceans. The group has a significant and complex fossil record, however, that indicates greater morphological diversity and wider geographic distribution in the Tertiary than today. This fossil record suggests that Nassariidae arose and diversified initially in the New World in the Late Cretaceous and Early Tertiary, spreading to Europe, Africa and beyond by Miocene times.

The genus *Bullia* s. s. is today an important and diverse component of the South African sandy shore molluscan fauna. The current status of *Bullia* s. s., however, is probably a relatively recent development. *Bullia* apparently did not reach Africa until the late Miocene or early Pliocene, and its approximately 40 living species are of Pliocene age or younger. Consideration of the phylogenetic and biogeographic history of the entire group suggests that the ancestors of modern *Bullia* s. s. may have reached Africa from South America via chance dispersal across open ocean, a mode usually not seriously considered for marine prosobranchs lacking a planktonic larval stage.

Among the last surviving representatives of the *Bullia* group in the North Atlantic were the late Miocene species of *Bullia* (*Bulliopsis*) from Maryland and Virginia. A morphological analysis of these species suggests that they show a variety of evolutionary modes. A new subspecies, *Bullia* (*Bulliopsis*) *quadrata bowlerensis*, is described. The phylogenetic relationships of these taxa to species of *Bulliopsis* from the lower Miocene of New Jersey and the Eocene of Alabama are explicitly evaluated for the first time.

An extension of the stratigraphic range of the species *Bullia* (*Bulliopsis*) *choctavensis* from Alabama is reported; instead of being limited to the lower Eocene Hatchetigbee Formation, it appears to extend from the upper Paleocene Nanafalia Formation.

The following genus-level taxa are considered to belong to the *Bullia* group: *Buccinanops*, *Buccinopsis*, *Bullia*, *Bulliopsis*, *Calophos*, *Colwellia*, *Desorinassa*, *Dorsanum*, *Keepingia*, *Pseudocominella*, and *Whitecliffia*. The generic names "*Cyllenina*" and "*Molopophorus*", as well as the systematic status of many of the species to which they have been applied, are of uncertain status and are used in an informal sense. The genus *Thanetinassa* may be intermediate between the *Bullia* group and other nassariids. A new species of the genus *Calophos*, *C. wilsoni* from the Pliocene of Florida, is described.

Methods of phylogenetic inference, particularly as applicable to fossil gastropods, are discussed. An informal method (the "faunal survey" method) for considering the effects of the completeness of the available fossil record on phylogenetic reconstruction is suggested. The fossil record is considered to be of unique and special importance in interpreting the evolutionary history of this group. A phylogenetic analysis of the family Nassariidae, based primarily but not exclusively on conchological characters, is presented, but the taxonomic position of several fossil and Recent groups remains unresolved. A classification for the group to the subgenus level, and a new subfamily, the Bulliinae, are proposed.

This paper points out a number of gastropod groups in need of detailed taxonomic study, and highlights the currently meager knowledge of the basic patterns of Cenozoic marine molluscan biogeography.

ACKNOWLEDGEMENTS

Over the protracted history of this project I have benefitted from the kindness of many people, in many places, without whose help this paper could not have assumed its present form. I am grateful to the following for all manner of assistance, guidance, suggestions and advice on matters large and small: at Dartmouth College, G. D. Johnson, F. L. Konopka, K. A. Korey, D. S. McCormick, and R. Neff; at the U. S. National Museum, F. J. Collier; at Harvard University, D. Backus, K. J. Boss, F. C. d'Escrivan, R. Dorit, R. C. Eng, M. J. Foote, D. H. Geary, S. J. Gould, R. I. Johnson, A. Kabat, W. P. Maddison, M. Matthewman, G. C. Mayer, M. Patterson, G. Rosenberg, R. M. Ross, and R. D. Turner. Many colleagues from many institutions generously answered unsolicited inquiries and provided me with a great deal of information on living and fossil representatives of the *Bullia* group, and associated problems: C. G. Adams [British Museum (Natural History)]; A. C. Brown [University of Capetown]; W. O. Cernohorsky [New Zealand Institute and Museum]; D. T. Dockery, III [Mississippi Geological Survey]; B. Kensley [U. S. National Museum]; R. A. Lutz [Rutgers University]; E. J. Moore [U. S. Geological Survey, Menlo Park, CA]; C. P. Nuttall [British Museum (Natural History)]; P. Penchaszadeh [Universidad Simon Bolivar, Caracas, Venezuela]; W. D. Pitt [California Academy of Sciences]; W. G. Siesser [Vanderbilt Uni-

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versity]; and W. J. Zinsmeister [Purdue University]. T. Collins [Yale University] and T. Cronin [U. S. Geological Survey, Reston, VA] provided valuable biostratigraphic information. R. T. Rye, II and D. Wilson [U. S. National Museum] provided early encouragement for this work. I am especially grateful to L. W. Ward, formerly of the U. S. Geological Survey, now at the Virginia Museum of Natural History, Martinsville, VA, for his advice and encouragement throughout this project. I thank K. J. Boss, A. C. Brown, W. O. Cernohorsky, D. T. Dockery, S. J. Gould, D. R. Lindberg, E. J. Moore, E. Nesbitt, C. P. Nuttall, W. G. Siesser, R. D. Turner, L. W. Ward, P. G. Williamson, W. J. Zinsmeister and two anonymous reviewers for reading all or parts of previous drafts, and for making many valuable comments and suggestions that substantially improved the manuscript. Any errors in or misinterpretations of fact that remain are of course wholly my own.

The following persons made specimens under their care or in their private collections available for study: W. Blow, T. Waller, and F. Collier [USNM]; R. Van Syoc [CAS]; D. R. Lindberg [UCMP]; E. Benamy [ANSP]; W. J. Zinsmeister [Purdue University]; L. Dolin [St. Denis, France]; A. M. Phillips, Jr. [LSU]; D. Bohaska [CMM]; D. C. Parris [NJSM]; P. R. Hoover [PRI], M. Carman [FMNH], and R. D. White [YPM]. J. Cooper and H. G. Owen [BM(NH)] kindly provided me with photographs of British Museum type specimens. A. C. Brown provided juvenile specimens of two Recent species of *Bullia* from South Africa.

I thank R. Dorit, G. Seiler, R. Allmon, K. Boss, and M. Olshan for timely translations from various non-Germanic languages. N. J. B. Aiello skillfully drew several of the figures. A. Colson assisted in digitizing. S. J. Gould and A. H. Knoll allowed me the freedom to pursue this project when I should have been doing other things.

Above all, I am grateful to my partner Robin Aiello Allmon for advice, patience, and support during this and other endeavors.

This work has been supported by a grant from the Paul K. Richter Memorial Trust at Dartmouth College, funds from the Department of Earth Sciences at Dartmouth College, the Department of Earth and Planetary Sciences at Harvard University and the Department of Invertebrate Paleontology of the Museum of Comparative Zoology, and a National Science Foundation Graduate Fellowship. Publication was made possible by funds from the College of Natural Sciences of the University of South Florida.

This paper is dedicated to the memory of Margaret C. Clark, who took me on my first trip to the Calvert Cliffs.

INTRODUCTION

Study Justification

The "*Bullia* group" (Brown, 1982, p. 309) refers here to a heterogeneous group of neogastropods in the family Nassariidae not assignable to the subfamilies Nassariinae or Cylleninae. Unlike their more familiar relatives, mudsnails of the genus *Nassarius* Duméril, 1806, living members of the *Bullia* group are never very common. Except in some localities in southern Africa and the Indian Subcontinent, they do not appear to form (or ever to have formed) a conspicuous or quantitatively important component of shallow marine faunas. Although living species of *Bullia* s. s. appear to be intricately adapted physiologically and behaviorally to their high-energy, nearshore environments (see, *e.g.*, Branch and Branch, 1981; Brown, 1982), members of the group are (and were) otherwise unremarkable morphologically. Their shells are typically simple buccinform, and lack notable or conspicuous features of form or sculpture.

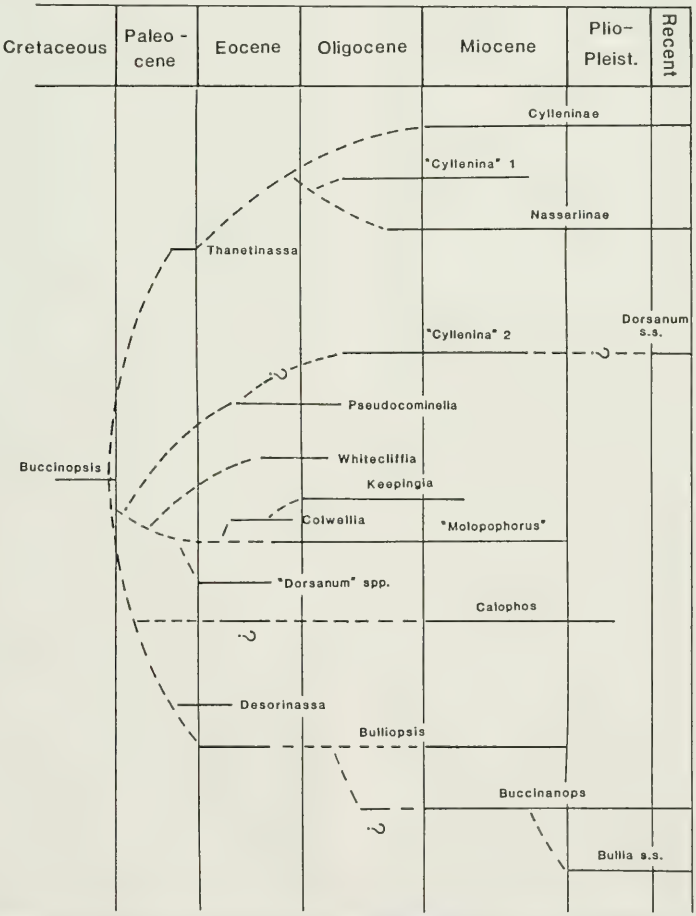
The *Bullia* group has long been something of a taxonomic wastebasket and systematic Cinderella. The generic names *Bullia* Gray, 1834, *Dorsanum* Gray, 1847 and *Buccinanops* d'Orbigny, 1841 (and several others) have been freely applied to a great number of living and fossil forms, usually on the basis of no more than similar overall shell form, and seldom with much attention to morphological details or possible phylogenetic relationships. These arbitrary classifications have prevented recognition of potentially interesting biogeographic patterns shown by members of the group, patterns that may apply to other Cenozoic molluscan taxa.

My approach to bringing some order to this group of snails is unconventional, and consists of three interconnected aspects. First, I present basic information on (to my knowledge) every fossil and living form previously connected by anyone with the name *Bullia*. To this extent this paper is a compilation and synopsis of all available information and published references on the group. I summarize these taxa geographically and stratigraphically, and suggest those which do and do not truly belong to the *Bullia* group. Several forms are also allied with the group here for the first time. Second, I discuss in detail the evolution of a small branch of the group, the species of *Bulliopsis* Conrad, 1862a from the Miocene of the Mid-Atlantic coastal plain of the U. S., tracing their relationships within the Cenozoic of North America as well as placing them in the larger context of the group as a whole. Third, I present a phylogenetic analysis of the *Bullia* group, paying particular attention to details of method and methodo-

logical assumptions. The paper is, to some extent, a test case for various phylogenetic methods as applied to fossil gastropods. Based on this analysis, I suggest a revised taxonomy of the group at the subgenus level, and a scenario for its biogeographic history.

This is a limited study. I have not personally examined large series of every taxon discussed, and this paper is, therefore, not a definitive systematic monograph of all these forms. It is a summary of current knowledge, a major result of which has been to highlight groups on which further work is required. As Mayr (1969, p. 259) has noted, "There is a time in the history of the study of each group of organisms in which one or the other kind of publication is most useful." I believe that the state of understanding of the taxa treated here is such that a critical review of all existing data, and the presentation of limited, testable phylogenetic and biogeographic hypotheses based on such a review, will best serve future research on the group.

A proposed phylogenetic tree of the family is shown in Text-figure 1. Its derivation and details are described beginning on p. 104. It is presented here in advance of that discussion as a convenient reference for the taxonomic sections that follow, and also as a graphical representation of a primary result of this review.



Text-figure 1.—Proposed phylogenetic tree for the evolution of the family Nassariidae, based on the cladogram presented in Text-figure 25. Solid lines represent known stratigraphic distributions of individual taxa; dashed lines represent inferred phylogenetic relationships.

SYSTEMATIC ZOOLOGY AND PALEONTOLOGY: INTRODUCTORY REMARKS

Systematic discussions in this paper focus on a variety of taxonomic levels, from the subspecies to the family. As differing amounts of information are available on different taxa, not all are examined at all levels. Only a single subgroup (*Bulliopsis* Conrad, 1862a) is analyzed here in great detail below the species level. Interrelationships of species are better understood in some groups (*e.g.*, *Calophos* Woodring, 1964) than others (*e.g.*, "*Molopophorus*" Gabb, 1869), although the recognized species of both kinds of groups are summarized. Several taxa (*e.g.*, *Buccinopsis* Conrad, 1857, *Desorinassa* Nuttall and Cooper, 1973, *Keepingia* Nuttall and Cooper, 1973, *Thanetinassa* Nuttall and Cooper, 1973, and *Whitecliffia* Nuttall and Cooper, 1973) are discussed only at the genus level, as summaries of their species can be found in other works. A thorough species-level study of living *Bullia* s. s. has never been undertaken, and is beyond the scope of this review. South African representatives of *Bullia* are treated here only at the subgenus level. Cernohorsky (1984) lists the 44 Recent species he considers valid, along with partial synonymies. The living South American species of *Buccinanops* are treated in some detail here for two reasons. They are fewer in number than the South African forms, including only seven species. More importantly, however, the geographic and stratigraphic distribution of the species of the *Bullia* group, as well as their morphological relationships, suggest that the living South American taxa occupy a more central position in the phylogeny of the group than do the South African taxa, which seem to be a relatively young side branch. An understanding of the South American forms may, therefore, be of substantial importance in understanding the group as a whole, and may allow future studies of interrelationships of the South African species to operate in a larger-scale phylogenetic context. The single Recent species of the genus *Dorsanum* Gray, 1847 and several other forms of uncertain affinities are also treated at the species level.

The generic and even the familial status of some forms discussed here remain unresolved. For example, although they are listed under their "traditional" genus and species designations, most of the taxa from the Paleogene of the Gulf Coastal Plain of the U. S. excluded from the *Bullia* group are of uncertain generic and familial positions. Although probably nassariid, the generic placement of species listed under "*Molopophorus*" is also unclear. The systematic position of fossils from the European Tertiary, most often placed in the genus *Dorsanum*, is similarly almost wholly undetermined, although it does appear that at least two and possibly three supraspecific taxa are represented. Treatment of these European forms here is at an indeterminate supraspecific level and for convenience all are referred to under the name "*Cyllenina*" [cf. *Cyllenina* Bellardi, 1882].

Quotation marks are used around generic and subgeneric names in this paper to indicate that the designation is known (or believed on firm grounds) to be incorrect or invalid, and that the listed species need to be placed under one or more other supraspecific names. Sometimes the generic name used in quotations will not be the original or even the most commonly employed, but is used for a particular purpose, usually some combination of familiarity and convenience. Explanations are provided in each case.

As both living and fossil taxa are discussed here, it ideally should have been possible to make comparisons between paleontological and neontological species concepts in this group. To some degree this has been the case. The Recent South American species *Bullia* (*Buccinanops*) *cochlidia* (Dillwyn, 1817) is highly variable in shell morphology, and this observation contributes to resolving the status of smaller but morphologically similar species of *Bullia* (*Bulliopsis*) from the Miocene of the Middle Atlantic United States. While radular, soft part, and opercular characters have been employed in resolving supraspecific relationships in living nassariids, however, species description and differentiation in this family continue to rely almost completely on conchological characters. In describing four new species of *Bullia* from the East African coast, for example, Kilburn (1978) refers briefly to the opercula and radulae of only three, those of the fourth being "unknown" even though the type specimens were obtained from a "dense colony . . . living in sand at low tide" (Kilburn, 1978, p. 297). Similarly, *Bullia rogersi* Smythe and Chatfield, 1981 is described solely from empty shells washed up on beaches. Thus, for this group, fossil species are in practice no more or less equivocal than living species.

After discussion of Recent species (pp. 12–29), fossil forms are summarized stratigraphically and geographically (pp. 29–90). For those Recent and fossil genera and subgenera that are nomenclaturally valid and believed to be fairly well-defined, new descriptions are given under the heading "Diagnosis". This applies to *Bullia* s. s., *Bullia* (*Buccinanops*), *Dorsanum*, *Bullia* (*Bulliopsis*) and *Calophos*. Other supraspecific groups are not so described for the reasons given in discussions prefacing their sections. These include *Buccinopsis* Conrad, 1857, "*Molopophorus*", and all European taxa.

New formal descriptions of individual species are given only for those for which sufficient material and occurrence data were available. This applies to Recent species of *Bullia* (*Buccinanops*) and *Dorsanum*, and fossil species of *Bullia* (*Bulliopsis*). Under the heading

"Remarks", all available information on morphological variability, occurrence, and comparisons with other taxa is summarized. This may consist only of comments on a published figure, but more often synthesizes observations of all examined specimens with previously published information.

For Recent taxa, data summarized under the heading "Occurrence" are derived largely from labels of specimens examined in the ANSP, USNM and MCZ collections. Locality names are presented as given on museum labels accompanying the specimens. For fossils, these data have usually been derived from a combination of museum labels, personally collected material, and published information. "Range" is stratigraphic range (usually to stage) as reported in the most authoritative sources available in each case. Type specimen(s), repository and localities are given in all cases for which these could be confirmed. Unless noted otherwise, type specimens, repositories and localities are unknown for all Recent species discussed. In lists of "Material examined", a question mark before a catalog number indicates that the identification of this specimen is uncertain.

In the plates specimens are figured in ventral (apertural) view unless otherwise noted.

Classification is used here to represent both cladistic (*i.e.*, branching order) and phenetic (*i.e.*, morphological divergence) information. Toward this end, systematic conclusions, as expressed in specific, subgeneric and generic assignments, are presented throughout this paper to facilitate discussion of these organisms. Classifications are summarized at three principal junctures. The first (p. 19) gives genus and species accounts for all living taxa. The second (p. 50) summarizes species and subspecies of *Bullia* (*Bulliopsis*) from the Miocene of Maryland, Virginia and New Jersey. Finally, all Recent and fossil supraspecific taxa in the *Bullia* group are listed in Table 16. Details and justification of these classifications are presented beginning on p. 100.

Institutional Abbreviations

ANSP: Academy of Natural Sciences, Philadelphia, PA, U. S. A.
BM(NH): Department of Palaeontology, British Museum (Natural History), London, England, U. K.
CAS: California Academy of Sciences, San Francisco, CA, U. S. A.
CMM: Calvert Marine Museum, Solomons, MD, U. S. A.
FMNH-UC: Field Museum of Natural History, Chicago, IL, U. S. A.
G-IGM: Museo de Paleontologia del Instituto de Geologia en la Cuidad Universitaria, Mexico City, Mexico.
GSATC: Geological Survey of Alabama Type Collection, Tuscaloosa, AL, U. S. A.
IRSNB: Institut Royal des Sciences Naturelles Belgique, Brussels, Belgium.
LACMIP: Department of Invertebrate Paleontology, Los Angeles County Museum, Los Angeles, CA, U. S. A.
LSU: Museum of Geoscience, Louisiana State University, Baton Rouge, LA, U. S. A.
MCZ(IP): Department of Invertebrate Paleontology, Museum of Comparative Zoology, Cambridge, MA, U. S. A.
MCZ(M): Department of Mollusks, Museum of Comparative Zoology, Cambridge, MA, U. S. A.
MGS: Mississippi Bureau of Geology, Jackson, MS, U. S. A.
MNHN: Museo Nacional de Historia Natural, Montevideo, Uruguay.
NHMB: Natural History Museum, Basel, Switzerland.
NJSM: New Jersey State Museum, Trenton, NJ, U. S. A.
PRI: Paleontological Research Institution, Ithaca, NY, U. S. A.
UA: University of Alaska, Fairbanks, AK, U. S. A.
UCMP: University of California Museum of Paleontology, Berkeley, CA, U. S. A.
UO: University of Oregon, Eugene, OR, U. S. A.
USGS: U. S. Geological Survey Collection, U. S. National Museum, Washington, DC, U. S. A., and National Center, Reston, VA, U. S. A.
USNM: U. S. National Museum of Natural History, Smithsonian Institution, Washington, DC, U. S. A.
UW: University of Washington, Seattle, WA, U. S. A.
YPM: Yale Peabody Museum, New Haven, CT, U. S. A.

Familial Classification

The suprageneric relationships of bucciniform neogastropods are very poorly understood, and this is reflected by instability in their family-level taxonomy. It is not clear that the conventionally recognized families represent monophyletic clades, and virtually nothing is known about their branching order relative to each other.

Although in some general sense the families Nassariidae (to which *Bullia* Gray, 1834 and its allies are now assigned) and Buccinidae (to which most were originally assigned) seem to form two readily distinguishable groups, it is difficult to list characters, especially of the shell alone, by which any given species may be placed unambiguously in one or the other group. Ponder (1973) has stated that while differentiation between these families is usually possible on the basis of shell and/or radular features, the "magnitude of the differences . . . is not great and there are practically no

anatomical features which can be used consistently to separate them." He adds that the groups "show levels of differentiation from one another that could be treated as subfamilial" (Ponder, 1973, p. 325).

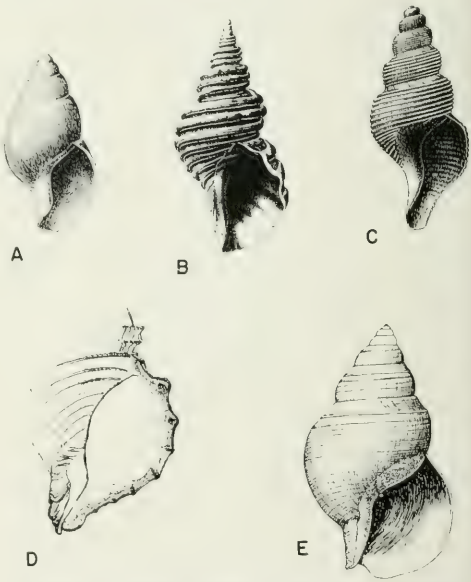
Cernohorsky (1984) agrees and states that it is a combination of characters, especially radular dentition, shape and size of the foot, and sometimes opercular and shell characters, "which enables us to segregate the Nassariidae from the Buccinidae and allows us to retain the family group name Nassariidae on conventional grounds" (Cernohorsky, 1984, p. 4).

In his summary descriptions of molluscan families, Boss (1982) suggests that nassariids typically are small to medium-sized (up to 50 mm total height), have short, indistinct anterior siphonal canals, and are mostly tropical or subtropical. Buccinids are described as typically larger (up to 150 mm) with more well-developed canals, and as being mainly temperate to boreal in their Recent distribution.

Following Wenz (1943), Nuttall and Cooper (1973) have suggested a number of distinctive shell characters by which nassariids may frequently be distinguished from buccinids. In typical nassariids, these authors note that:

> growth lines on the neck region are bent aborally to form a ridge confluent with the adapical margin of the track of the anterior notch. The deepest point of the asymmetrically U-shaped notch is usually fairly close to the ridge. Below the ridge there is some variation. The growth lines range from regular to imbricate and are reverse S-shaped, but the upper and lower halves of the S may be of varying proportions and curvature. (Nuttall and Cooper, 1973, p. 181).

Nuttall and Cooper also suggest that in most nassariids the columella bears a terminal plait or fold (see, *e.g.*, Pl. 1, figs. 1–3). The exact structure of, and recognition of homology in the terminal columellar fold of bucciniform gastropods is a complex problem, one that cannot be explored fully here. The terminal columellar fold shown by most nassariids is a single, smooth, but sharp and distinct infolding of the edge of the shell at the end of the columella, continuing up the columella as a single ridge-and-fold structure on the anterior of the whorl. The surrounding area of the columella and fasciole is relatively simple in many nassariids, and more complexly folded or imbricated in others. The anterior end of the columella may be bent to the left, creating an even more distinctly folded form, or may be straight with the fold visible only by looking into the aperture at an angle or by sectioning the shell. Only a minority of living species of *Bullia* s. s. from South Africa show a pronounced terminal columellar fold, and their columellae are relatively simple. Almost all species of *Nassarius* Duméril, 1806, show some sort of terminal columellar fold, but it is not clear that these are all the same structure developmentally. Within Recent and fossil Buccinidae s. l., the anterior columella takes almost every conceivable form (Text-fig. 2). Species of a number of genera have relatively elongate anterior canals bounded by relatively simple unfolded columellae (*e.g., Colus* Röding, 1798, *Neptunea* Röding, 1798). Others have relatively short anterior canals and columellae bearing distinct terminal columellar folds and more complex structures (*e.g. Northia* Gray, 1847 [see Pl. 12, fig. 2], *Phos* Montfort, 1810 [see Pl. 12, fig. 2]).



Text-figure 2.—Sketches of species of Buccinidae s. l., suggestive of the range of variability in the group, and illustrating some conchological characters which distinguish nassariids from buccinids. **A**, *Colus aphelus* (Dall, 1890), eastern Pacific. Shell lacks conspicuous external sculpture, and has a simple anterior columella bent slightly to the animal's left. Apertural view. Size not given. (from Abbott, 1974) **B**, *Beringius crebricostatus* (Dall, 1877), Alaska. Shell bears conspicuous external spiral sculpture which is reflected by broad grooves on the interior of the aperture. Anterior columella simple and lacking any terminal fold. Apertural view. Approx. 11 cm total height. (from Abbott, 1974) **C**, *Colus sapius* (Dall, 1919), Alaska. Shell bears relatively fine external spiral sculpture reflected inside the aperture, and a very simple anterior columella. Apertural view. Size not given. (from Abbott, 1974) **D**, *Neptunea lyrata decemcostata* (Say, 1827), New England. This shell is relatively thick, bears broad, conspicuous external spiral sculpture reflected inside the aperture, and shows a complexly folded anterior columella that is twisted sharply to the animal's left and shows a slight terminal fold. Apertural view. 74 mm total height. (original drawing by N. J. B. Aiello) **E**, *Buccinum pemphigus* Dall, 1907, Bering Sea. Shell relatively thin, lacking conspicuous internal or external sculpture. It has a simple anterior columella, and shows slight subsutural shouldering. Apertural view. 63 mm total height. (from Abbott, 1974)

While it is generally true that most buccinids are heavier and more robust than most nassariids, there are a number of fragile, thin-shelled species in Buccinidae and some South American *Bullia* group species that are heavier than most buccinids. Both groups include high- and low-spired forms, and species with and without posterior slits or sinuses. It is almost certainly true that mean total height of nassariids is lower than that of buccinids. Buccinids typically show pronounced spiral and axial external sculpture, but many species are almost completely smooth. A large proportion of Recent species of *Nassarius* have conspicuously beaded or cancellate sculpture, and most living *Bullia* group species lack profound external sculpture. Subsutural shelves or carinae are present in both groups, although most buccinids have more rounded, convex whorls. Most species of *Nassarius* have a well-developed parietal callus, frequently marked by a vertical plait or ridge parallel to the aperture and usually separated from the columella by a deep slit. The callus is present as a faint to moderate wash on the columella in almost all buccinids. The presence of striations, denticles or ridges on the inside of the outer apertural lip is variable in both Nassariidae and Buccinidae s. l. In most buccinids showing such features, however, these elements are direct reflections of spiral sculpture on the outside of the lip (see Text-fig. 2). No definite nassariid shows this pattern.

In this paper substantial importance is placed on the presence of a terminal columellar fold as a diagnostic character of Nassariidae. It is clear, however, that this is not a perfectly reliable character for the family, and other conchological characters are also employed as applicable.

Nassariidae and Buccinidae are conventionally placed in a superfamily, called Buccinacea or Muricacea (or Muricoidea; see Ponder and Warén, 1988) depending upon what other families are included [compare Taylor and Sohl (1962) with Ponder (1973)], but the phylogenetic position and most appropriate taxonomic arrangement of these and related suprageneric groups have been controversial. Mainly on the basis of radular and opercular characters, Powell (1929) proposed that what may be referred to as the "buccinoids" (= Buccinidae s. l.) be divided into four families: Buccinidae s. s., Neptuniidae, Buccinulidae and Cominellidae. This arrangement has been accepted by several later authors [*e.g.*, Fleming (1966)]. In 1951, Powell revised this classification slightly, including cominellids as one of three subfamilies in Buccinulidae. Thiele (1929, pp. 305–319) included all of the buccinoid genera in a single family Buccinidae. Ponder (1973, p. 325) concurs with this classification and states that the differences in radulae and opercula upon which Powell's suprageneric taxa are based "seem very minor when the total variation within the group is considered, and should not be recognized even as subfamilies." Most recent discussions of neogastropod classification (*e.g.*, Abbott, 1974; Taylor, Morris, and Taylor, 1980; Boss, 1982) recognize only Buccinidae, although Davies and Eames (1971) recognize Neptuneidae, and Sepkoski (1982) lists Buccinidae, Buccinulidae, and Neptuneidae as separate families.

Buccinidae s. l. includes as many as 175 Recent genera (Taylor and Sohl, 1962), and at present has a wide geographic distribution, concentrated in high latitudes. Powell (1951, pp. 131–132) suggested that "none of the Antarctic and subantarctic whelks appears to have much in common with the northern *Buccinum* . . . ." and viewed Buccinulidae as an endemic southern hemisphere group that may have evolved there "concurrently with the northern Buccinidae and Neptuniidae, a common ancestry being assumed in the geological past." There is evidence that the importance of buccinoids in high latitudes has developed relatively recently, probably since the late Miocene (Briggs, 1970; Nelson, 1978; Franz and Merrill, 1980; Taylor, Morris, and Taylor, 1980). Nelson (1978) has shown that the genus *Neptunea* Röding, 1798 is probably of more recent origin than had been thought previously, arising in the Pacific in the late Oligocene.

It is, therefore, probable that: (1) the family Buccinidae s. l. is artificial and polyphyletic; (2) many or most pre-Neogene species (as well as many Recent species) commonly assigned to Buccinidae are best allocated to other family-level taxa, some of which may be closer to Nassariidae than to Buccinidae s. s.; and (3) Buccinidae s. s. (*e.g.*, *Buccinum* Linnaeus, 1758) may be descended from Nassariidae rather than from earlier buccinoid forms (Nuttall, written commun., 1985), and should, therefore, not be viewed as representing morphologies primitive relative to nassariids.

In the study of these gastropods it has, furthermore, been the tendency to attempt to place all Late Mesozoic and Early Tertiary forms into a few traditionally recognized living families. This has led to an obscuring of family-level phylogeny and may have substantially underestimated family-level diversity during this period.

Cernohorsky (1984) divides the family Nassariidae into three subfamilies: Nassariinae, containing the genera *Nassarius* Duméril, 1806 [including the familiar American mudsnail *Ilyanassa* Stimpson, 1865, as a subgenus (see Pl. 1, figs. 1, 2)], *Hebra* Adams and Adams, 1853, and *Demoulia* Gray, 1838; Cylleninae, containing *Cyllene* Gray, 1834 (see Pl. 1, figs. 3, 9), and *Cyllenina* Bellardi, 1882 (the latter known only from the Neogene of Western Europe; see discussion

of these forms on pp. 83–86); and Dorsaninae, containing most of the forms included here in the "*Bullia* group". Cernohorsky suggests that Dorsaninae is the oldest of these three subfamilies, and that it may have arisen "from a buccinid ancestor" in the earliest Tertiary. Nassariinae, he suggests, may have arisen sometime during the Paleocene from a species of *Brachysphingus* Gabb, 1869, and Cylleninae from a species of *Molopophorus* Gabb, 1869, in the later Paleogene. *Brachysphingus* and *Molopophorus* are both considered by Cernohorsky to belong to Buccinidae (see discussion of these taxa on pp. 63, 64); he, therefore, seems to believe that the family Nassariidae is polyphyletic, with each of its subfamilies derived independently from branches of Buccinidae s. l.

In summary, it is not clear that Nassariidae or Buccinidae, as usually recognized, represent coherent evolutionary entities (*i.e.*, monophyletic clades), or, if they do, whether they are distinguishable conchologically at the family level from each other or from other closely related groups. The branching order of these groups is also unknown, and so it is unclear which among them is most closely related to the nassariids, and so to the *Bullia* group.

The *Bullia* Group and Melanopsids

As noted on p. 30, Conrad's final (1866b) redesignation of Miocene species of *Bulliopsis* Conrad, 1862a was to the mesogastropod genus *Melanopsis* Ferussac, 1807, a taxon known from fossil and Recent representatives from Europe and the Mediterranean. Fischer (1887) agreed with this assignment.

Species of *Melanopsis* from Tertiary deposits of Western and Central Europe do indeed show a striking degree of resemblance to species of *Bullia* (*Bulliopsis*) from the Maryland and Virginia Miocene, and it is easy to see the source of Conrad's confusion. There are few conchological characters that allow consistent discrimination of *Melanopsis* from Europe and *Bullia* group species from North and South America or elsewhere (Allmon and Geary, 1986). Most, but not all melanopsids, show a broad, rounded, corona-like ridge in the middle of the adapical half of the body whorl, usually associated with a depressed area adapically. This feature is absent in *Bullia* group species. Most, but not all *Bullia* group species show the terminal fold on the columella, and this is generally lacking in melanopsids, in which the anterior portion of the columella forms a simple blunt or tapering projection.

It is largely on the basis of two non-morphological observations that these two groups of gastropods can be separated in the fossil record. First, no fossil or Recent melanopsids are known to be fully marine (Geary, 1986). Second, the distribution of fossil melanopsids is exclusively Tethyan and Paratethyan and that of living species primarily Mediterranean. If these non-morphological observations were not available, it would be difficult to exclude fossil melanopsids from consideration in a study of the evolutionary history of the *Bullia* group.

RECENT REPRESENTATIVES

Ecology

Although substantial work has been done on the ecology and soft part morphology of a few living species of the *Bullia* group, little is known about most species. Brown (1982) summarizes physiological and behavioral studies on South African *Bullia*. Ansell and Trevallion (1969, 1970), Trevallion *et al.* (1970), and Ansell *et al.* (1972) have described aspects of the ecology of *Bullia melanoides* (Deshayes, 1832) from India. There appears to be no published information on the ecology of *Dorsanum miran* (Bruguière, 1789) from West Africa, aside from the observations of Longhurst (1958), who states that this species is found in 7–16 m off the coast of Senegal on silty to shelly sands. Buchanan (1958, p. 17) and Gauld and Buchanan (1956) have briefly discussed the environment of *Bullia*? *granulosa* (Lamarck, 1822) from West Africa. The studies of Penchaszadeh (1971a, 1971b, 1973) are the only published sources of detailed information on the ecology of South American species.

South African species of *Bullia* Gray, 1834 are similar to species of *Nassarius* Duméril, 1806, in being opportunistic, carnivorous scavengers (Brown, 1982). Intertidal species seem to rely mainly on stranded coelenterates such as jellyfish and siphonophores, but may feed on almost any beached animal matter (even, for example, sea snakes [Branch and Branch, 1981, p. 54]). South African *Bullia* are eyeless. Much of their feeding behavior, particularly of intertidal species, seems to be dependent upon olfaction (Brown, 1971), and the osphradium is well developed (Brown and Noble, 1960; Newell and Brown, 1977).

Penchaszadeh (1971a) has reported that, in captivity, the South American species *Buccinanops monilifer*um (Kiener, 1834) will accept a wide range of foods, including prawns, crayfish, amphipods and mussels. *B. monilifera* appears to be an active burrower in sandy substrates at depths of 5–15 m. *B. duartei* Klappenbach, 1961 is a very shallow to intertidal species, while *B. globulosum* (Kiener, 1834) is mainly subtidal; *B. cochlidium* (Dillwyn, 1817) occurs at depths of 5–15 m (Penchaszadeh, written commun., 1985).

Despite many physiological and behavioral adaptations to their habitat, the shells of living species of *Bullia* s. s. do not appear to reflect in any detailed way their modes of life. South African species, often called

"plough snails" because of their large foot, are divisible into two ecological groups. The predominantly intertidal species regularly crawl and feed on sandy beaches and "exploit wave action and currents by spreading their broad, thin, agile feet and surfing up and down the shore" (Brown, 1982, p. 311). The predominantly subtidal species do not surf and are found above the low tide mark only on the most sheltered beaches (Brown, written commun., 1986). The following species are predominantly intertidal and frequently display surfing behavior (Brown, 1982; Kilburn and Rippey, 1982): *B. digitalis* (Dillwyn, 1817), *B. rhodostoma* Reeve, 1847 (see Pl. 2, fig. 3 herein), *B. pura* Melvill, 1885, *B. vittata* (Linnaeus, 1767)[see Pl. 2, fig. 7 herein], *B. melanoides* (Deshayes, 1832), *B. natalensis* (Krauss, 1848). The following species are predominantly sublittoral and are not known to surf: *B. laevissima* (Gmelin, 1791)[see Pl. 2, fig. 6 herein], *B. tenuis* Reeve, 1846 (see Pl. 2, fig. 2 herein), *B. annulata* (Lamarck, 1816a)[see Pl. 2, fig. 5; Pl. 5, figs. 1, 2 herein], *B. diluta* (Krauss, 1848), *B. callosa* (Wood, 1828). Comparison of habit with shell form indicates that surfing species tend to be relatively elongate, smooth and relatively thin-shelled, and are perhaps less variable in their shell form as a group than nonsurfing species. Brown (1982, p. 311) points out that a relatively massive and heavy shell, such as that of the subtidal species *B. laevissima*, would be disadvantageous for an actively surfing species such as *B. digitalis*. He observes further that *B. rhodostoma* surfs higher up the shore than *B. digitalis* and has a still lighter shell with lower specific gravity. Among intertidal species, however, the heavier shell of *B. digitalis* may give it greater stability and thus better opportunities for feeding under high energy conditions (McGwynne, 1980). A very heavy, low-spired form, such as that of *B. laevissima*, is not shared by other subtidal species, such as *B. tenuis* and *B. annulata*.

Previous Taxonomic Work

A representative of the *Bullia* group was first described and figured by Chemnitz (*in* Martini and Chemnitz, 1795, p. 275) as *Buccinum Cochlidium*, which he described as a "land snail" collected on Captain Cook's voyages to the "South Seas and Bougainville", but which in fact almost certainly came from the Atlantic coast of southern South America, an area also visited briefly by Cook in 1768 and 1774 (Villiers, 1967). Apparently without reference to additional material, Dillwyn (1817, p. 627) also listed *Buccinum cochlidium* as a land snail inhabiting the "islands of the South Seas". Chemnitz's work has been ruled nonbinomial and so without nomenclatural priority (Hemming, 1958). Therefore, Dillwyn's description and use of the name, although taken virtually verbatim from Chemnitz, is the oldest valid citation.

Kiener (1834, p. 10) also listed *Buccinum cochlidium* as occurring in the South Seas, particularly around New Zealand. He treated a total of 108 species of the genus *Buccinum* Linnaeus, 1758, and described a number of new species including *B. lamarckii*, *B. globulosum*, *B. paytense*, and *B. moniliferum*, all of which were eventually included in the *Bullia* group.

The genus *Bullia* was first designated in a plate caption (pl. 37, fig. 8, as *Bullia semiplicata*) in Griffith and Pidgeon's 1834 translation of Cuvier's *Animal Kingdom*. J. E. Gray is associated with the genus name only in the *Index* (p. 596), where it is misspelled "*Bullaea*". Not until 1839 did Gray actually describe the genus, in order to distinguish, in the words of Reeve (1846), "a very natural group of species intermediate between *Buccinum* and *Terebra*." *Bullia semiplicata* Gray, 1834 is a junior synonym of *Buccinum callosum* Wood, 1828 (Cernohorsky, 1984, p. 22; see Pl. 2, fig. 1 herein).

In 1841, d'Orbigny erected the genus *Buccinanops* and placed in it the South American species *Buccinum globulosum* Kiener, 1834 and *Buccinum cochlidium* Dillwyn, 1817. The genus *Dorsanum* was established by Gray (1847, p. 139) for the species *Buccinum politum* Lamarck, 1822, a junior synonym of *Buccinum miran* Bruguière, 1789. Gray himself seems not to have published a description of *Dorsanum*; Chenu (1859, p. 160) and Fischer (1884, p. 635) appear to have been the first to provide formal descriptions of this taxon.

The subsequent taxonomic history of these gastropods has been highly unstable and marked by no real progress in understanding the relationships among the species. Generic- and subgeneric-level taxa have been repeatedly rearranged, usually with little or no explicit justification for the preference of one arrangement over another. The major classifications are summarized in Table 1, and illustrate the often arbitrary nature of taxonomic decision-making in the study of the group.

Systematic Characters in Recent Species

Five principal potential sources of information are available to help in analyzing the relationships of these animals: (1) soft part morphology; (2) form of the radula; (3) form of the operculum; (4) mode of reproduction; and (5) shell form and sculpture, including form of the protoconch and early teleoconch.

Soft parts.—Little is known about comparative internal anatomy of living members of the *Bullia* group, and the soft-part characters most often mentioned are external. Of these, the great size of the expanded foot is most conspicuous. In *Bullia* s. s., the posterior of the foot bears two "metapodial tentacles", while these tentacles are absent in *Dorsanum* s. s. (Cernohorsky, 1984, pp. 22–23). South American species of *Buccinanops* have only a single metapodial tentacle (see illustrations

in Gray, 1850; Penchaszadeh, 1971a; Cernohorsky, 1984).

Another conspicuous characteristic of *Bullia* s. s. is that it is eyeless as an adult. In *B. digitalis* (Dillwyn, 1817), eyespots are present in the veligers (da Silva and Brown, 1985). Adult specimens of *Buccinanops paytense* (Kiener, 1834) and *B. moniliferum* (Kiener, 1834) from South America also lack any trace of eyes (Penchaszadeh, written commun., 1985; personal observation of preserved material, MCZ(M) collection). Eyes are apparently present in *Dorsanum miran* (Bruguière, 1789) and in *Adinopsis skoogi* Odhner, 1923 (Barnard, 1959; Cernohorsky, 1984). Cephalic tentacles also differ among supraspecific groups, being long and slender in *Bullia* s. s. (and *Buccinanops* ?), but relatively short in *Dorsanum* (Cernohorsky, 1984).

Radula.—Cernohorsky (1984, p. 23) states that the radulae of most species of *Buccinanops* are generally similar to those of species of *Bullia* s. s., but that the radula of *Dorsanum miran* (Bruguière, 1789) differs from those in *Buccinanops* and *Bullia* s. s., particularly

Table 1.—Previous classifications of the *Bullia* group.

Adams and Adams (1853)
- Genus *Bullia* Gray, 1834
  - Subgenus *Bullia* Gray, 1834
  - Subgenus *Buccinanops* d'Orbigny, 1841
- Genus *Pseudostrombus* Mörch, 1852[1]
  - Subgenus *Pseudostrombus* Mörch, 1852[2]
  - Subgenus *Leiodomus* Swainson, 1840
  - Subgenus *Adinus* Adams and Adams, 1853

Chenu (1859)
- Genus *Bullia* Gray, 1834
  - Subgenus *Bullia* Gray, 1834
  - Subgenus *Buccinanops* d'Orbigny, 1841
  - Subgenus *Dorsanum* Gray, 1847[3]
  - Subgenus *Leiodomus* Swainson, 1840
  - Subgenus *Adinus* Adams and Adams, 1853

Fischer (1884)
- Genus *Dorsanum* Gray, 1847
  - Subgenus *Dorsanum* Gray, 1847
  - Subgenus *Leiodomus* Swainson, 1840
  - Subgenus *Adinus* Adams and Adams, 1853
  - Subgenus *Northia* Gray, 1847
- Genus *Buccinanops* d'Orbigny, 1841
  - Subgenus *Buccinanops* d'Orbigny, 1841
  - Subgenus *Bullia* Gray, 1834

Cossmann (1901b)
- Subfamily Dorsaninae Cossmann, 1901b
- Genus *Dorsanum* Gray, 1847
- Genus *Buccinanops* d'Orbigny, 1841
  - Subgenus *Buccinanops* d'Orbigny, 1841
  - Subgenus *Bullia* Gray, 1834
  - *Subgenus *Brachysphingus* Gabb, 1869

Thiele (1929–1931)
- Genus *Bullia* Gray, 1834
  - Subgenus *Bullia* Gray, 1834
  - Subgenus *Dorsanum* Gray, 1847

Peile (1937)
- Genus *Bullia* Gray, 1834
- Genus *Cereobullia* Melvill and Peile, 1924
- Genus *Leiodomus* Swainson, 1840
- Genus *Buccinanops* d'Orbigny, 1841
- Genus *Dorsanum* Gray, 1847
- Genus *Adinopsis* Odhner, 1923

Wenz (1943)
- Genus *Dorsanum* Gray, 1847
  - Subgenus *Dorsanum* Gray, 1847
  - Subgenus *Adinus* Adams and Adams, 1853
  - Subgenus *Cereobullia* Melvill and Peile, 1924
  - *Subgenus *Sagenella* Conrad, 1865a
- Genus *Bullia* Gray, 1834
  - Subgenus *Bullia* Gray, 1834
  - *Subgenus *Anbullina* Palmer, 1937
  - Subgenus *Buccinanops* d'Orbigny, 1841
  - *Subgenus *Lisbonia* Palmer, 1937
- *Genus *Monoptygma* Lea, 1833
- *Genus *Molopophorus* Gabb, 1869
- *Genus *Brachysphingus* Gabb, 1869
- *Genus *Bulliopsis* Conrad, 1862a

Barnard (1959)[4], Nickles (1950), Adam and Knudsen (1984)
- Genus *Bullia* Gray, 1834[5]

Cernohorsky (1982)
- Genus *Bullia* Gray, 1834
  - Subgenus *Bullia* Gray, 1834
  - Subgenus *Adinopsis* Odhner, 1923
  - Subgenus *Adinus* Adams and Adams, 1853
  - Subgenus *Buccinanops* d'Orbigny, 1841
  - *Subgenus *Bulliopsis* Conrad, 1862a
  - *Subgenus *Bullovia* Palmer, 1937
  - Subgenus *Cereobullia* Melvill and Peile, 1924
  - Subgenus *Dorsanum* Gray, 1847

Cernohorsky (1984)
- Genus *Bullia* Gray, 1834
  - Subgenus *Bullia* Gray, 1834
  - Subgenus *Cereobullia* Melvill and Peile, 1924
- Genus *Buccinanops* d'Orbigny, 1841
- Genus *Dorsanum* Gray, 1847
  - Subgenus *Dorsanum* Gray, 1847
  - Subgenus *Fluviodorsum* Boettger, 1885[6]
- *Genus *Bulliopsis* Conrad, 1862a
- *Genus *Desorinassa* Nuttall and Cooper, 1973
- *Genus *Anbullina* [sic] Palmer, 1937
- ?*Genus *Lisbonia* Palmer, 1937

* Taxa known only from fossils.

[1] The name *Pseudostrombus* was first proposed by Klein (1753). Mörch (1852) is the first post-Linnaean use.

[2] Adams and Adams included the type species of *Dorsanum, Dorsanum politum* (Lamarck, 1822) [= *Dorsanum miran* (Bruguière, 1789)], in the subgenus *Pseudostrombus*.

[3] Chenu included *Pseudostrombus* under *Dorsanum*.

[4] Brown (1971, 1982) and Adam and Knudsen (1984) erroneously cite Barnard (1959) as considering *Dorsanum* and *Bullia* as separate genera.

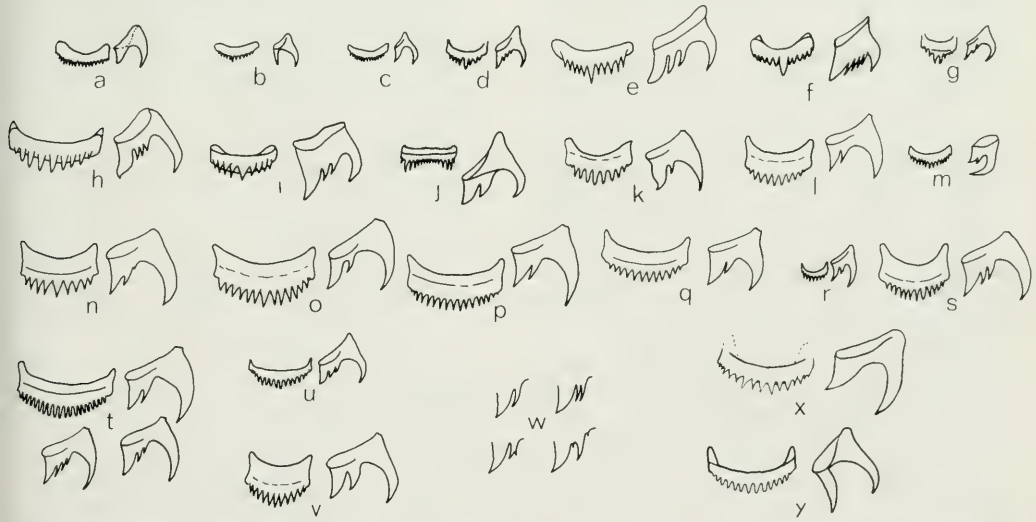
[5] The single genus *Bullia* is not divided into subgenera by these authors, but is considered to include species assigned to *Dorsanum* and *Leiodomus*. These authors considered only Recent African species.

[6] The subgenus *Fluviodorsum* includes the species listed in this paper as *Bullia* ? *granulosa* (Lamarck, 1822).

in having bicuspid lateral teeth. Rios and Calvo (1984), on the other hand, have claimed that in *Buccinanops*, the rachidian teeth generally tend to decrease in size toward the sides and the lateral teeth are usually multicuspidate, while in *Bullia* s. s., rachidian teeth are usually equal-sized with bicuspidate laterals. In those species for which radular morphology is known, this radular pattern seems to hold in general for species of *Buccinanops*, but less so for species of *Bullia* s. s., in which the lateral teeth may be multicuspidate in some species. Barnard (1962), citing the work of Peile, states that considerable variation occurs in the lateral teeth of South African species of *Bullia*, even within an individual. Text-figure 3 suggests substantial variation within many species and genera. It seems, however, that the lateral teeth of *Dorsanum* s. s. are consistently bicuspidate, in this being similar to those of most species of *Nassarius* Duméril, 1806 (although some species of *Nassarius* are themselves highly variable, at least one having both bi- and multicuspidate laterals [Nesbitt, written commun., 1987]). The laterals of *Bullia* s. s. and *Buccinanops* in contrast, are almost always multicuspidate.

Operculum.—Opercula show a great deal of variation within species and genera (Text-fig. 4), and as a result are of limited utility in indicating supraspecific relationships. In *Bullia* s. s. from South Africa, opercula can be either smooth or denticulate at the margin, and can vary in relative size, from almost filling the aperture in some species to hardly noticeable in others. The operculum of *Dorsanum miran* (Bruguière, 1789) is always small and smooth at the margin (Fischer, 1884; Adam and Knudsen, 1984). Opercula of South American species of *Buccinanops* are apparently all smooth-margined and relatively large.

Mode of Reproduction.—The larvae of *Bullia* s. s. from South Africa are all apparently nonplanktonic and nonplanktotrophic (*sensu* Jablonski and Lutz, 1983; Turner, Pechenik, and Calloway, 1986). The eggs of all species so far investigated produce crawling young,

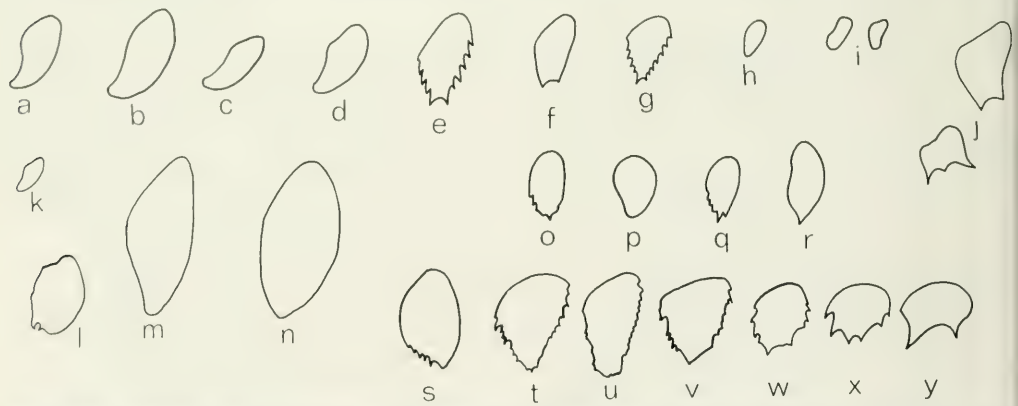


Text-figure 3.—Radular dentitions of living species in the *Bullia* group. **a**, *Bullia* ? *granulosa* (Lamarck, 1822) (from Adam and Knudsen, 1984); **b**, *Dorsanum miran* (Bruguière, 1789) (from Peile, 1937); **c**, *Dorsanum* ? *terebraeforme* (Dautzenberg, 1913) (from Peile, 1937); **d**, *Bullia* (*Buccinanops*) *globulosa* (Kiener, 1834) (from Peile, 1937); **e**, *Bullia* (*Buccinanops*) *deforme* (King and Broderip, 1831) (from Carcelles and Parodiz, 1939); **f**, *Bullia* (*Buccinanops*) *monilifera* (Kiener, 1834) (from Carcelles and Parodiz, 1939); **g**, *Bullia* (*Buccinanops*) *cochlidia* (Dillwyn, 1817) (from Peile, 1937, there as *gradata*); **h**, *Bullia* (*Buccinanops*) *uruguayensis* Pilsbry, 1897b (from Carcelles and Parodiz, 1939); **i**, *Bullia* (*Buccinanops*) *cochlidia* (Dillwyn, 1817) (from Carcelles and Parodiz, 1939, there as *gradatum*); **j**, *Bullia* (*Cereobullia*) *ceroplasta* (Melvill and Peile, 1924) (after Peile, 1937); **k**, *Bullia* (*Bullia*) *pura* Melvill, 1885 (from Barnard, 1959); **l**, *Bullia* (*Bullia*) *natalensis* (Krauss, 1848) (from Barnard, 1959); **m**, *Bullia* (*Cereobullia*) *ceroplasta* (Melvill and Peile, 1924) (from Melvill and Peile, 1924); **n**, *Bullia* (*Bullia*) *tenuis* Reeve, 1846 (from Barnard, 1959); **o**, *Bullia* (*Bullia*) *annulata* (Lamarck, 1816a) (from Barnard, 1959); **p**, *Bullia* (*Bullia*) *digitalis* (Dillwyn, 1817) (from Barnard, 1959); **q**, *Bullia* (*Bullia*) *mozambicensis* Smith, 1878 (from Barnard, 1959); **r**, *Bullia* (*Bullia*) *annulata* (Lamarck, 1816a) (from Peile, 1937); **s**, *Bullia* (*Bullia*) *rhodostoma* Reeve, 1847 (from Barnard, 1959); **t**, *Bullia* (*Bullia*) *laevissima* (Gmelin, 1791) (from Barnard, 1959); **u**, *Bullia* (*Bullia*) *laevissima* (Gmelin, 1791) (from Peile, 1937); **v**, *Bullia* (*Bullia*) *similis* Sowerby, 1897 (from Barnard, 1959); **w**, *Bullia* (*Bullia*) *similis* Sowerby, 1897 variants (from Barnard, 1959); **x**, *Nassarius arcularia arcularia* (Linnaeus, 1758) (from Cernohorsky, 1984); **y**, "*Adinopsis*" *skoogi* Odhner, 1923 (from Peile, 1937).

with veliger stages being passed within the egg or egg capsule (Ansell and Trevallion, 1970; Brown, 1982, 1985; da Silva and Brown, 1985). There is considerable variation, however, in the details of reproduction and development among living species. The South African species *B. digitalis* (Dillwyn, 1817) "packages" its eggs in two different ways; clusters of up to 1500 eggs may be contained in a single large mucus sheath and deposited four to 12 cm below the sand surface, or clusters of approximately 150 eggs may be contained in their own capsules and held on the ventral surface of the maternal foot (Brown, 1982; da Silva and Brown, 1985). In the latter case as many as 40,000 minute eggs may be produced at one time (da Silva and Brown, 1985). *Bullia tenuis* Reeve, 1846, on the other hand, produces approximately 60 egg capsules at a time, each containing only a single developing egg. The young may be as large as 5 mm at hatching (da Silva and Brown, 1985; Brown, 1985).

In the tropical Indian species *Bullia melanoides* (Deshayes, 1832), egg capsules contain one to five developing embryos and a much larger number of nutritive nurse eggs (Ansell and Trevallion, 1970). In most species of *Bullia* s. s. that have been studied [*i.e.*, *B. tenuis* Reeve, 1846, some *B. digitalis* (Dillwyn, 1817), *B. melanoides* (Deshayes, 1832), *B. vittata* (Linnaeus, 1767), *B. tranquebarica* (Röding, 1798)], the egg cases are carried on the ventral surface of the female's foot [up to 33 capsules reported in *B. melanoides*] (Ansell and Trevallion, 1970; Brown, 1982, 1985; da Silva and Brown, 1985; Jayabal, Thilaga, and Kalyani, 1987). Brown (1985) has suggested that this pattern is typical of all *Bullia* species. From these capsules emerge fully formed, actively crawling, miniature adults. *Bullia nuttalli* Kilburn, 1978, is reported to hold the eggs within the female's body until hatching (Kilburn, 1978).

A similar pattern appears to hold for species of *Buccinanops* from South America (Penchaszadeh, 1971a, 1971b, 1973). These species, however, carry the egg capsules attached to the callus region of the parental shell by a short peduncle. Penchaszadeh (1971a) reports that in *Buccinanops moniliferum* (Kiener, 1834) there may be up to 21 egg cases attached to a single shell. In each of these capsules only a single embryo develops, hatching in the crawling stage. Each capsule may contain up to 1600 nurse eggs to nourish this one embryo. This also appears to apply to *B. globulosum* (Kiener, 1834), *B. deformis* (King and Broderip, 1831),



Text-figure 4.—Opercular outlines of living species of the *Bullia* group. **a**, *Bullia* (*Bullia*) *rhodostoma* Reeve, 1847 (9.0 × 3.8 mm) (from Barnard, 1959); **b**, *Bullia* (*Bullia*) *natalensis* (Krauss, 1848) (5.0 × 2.5 mm) (from Barnard, 1959); **c**, *Bullia* (*Bullia*) *mozambicensis* Smith, 1878 (6.5 × 3.0 mm) (from Barnard, 1959); **d**, *Bullia* (*Bullia*) *pura* Melvill, 1885 (4.5 × 2.75 mm) (from Barnard, 1959); **e**, *Bullia* (*Bullia*) *simulis* Sowerby, 1897 (6.0 × 3.5 mm) (from Barnard, 1959); **f**, *Bullia* (*Bullia*) *osculata* Sowerby, 1900 (3.5 × 2.0 mm) (from Barnard, 1959); **g**, *Bullia* (*Bullia*) *digitalis* (Dillwyn, 1817) (6.0 × 3.8 mm) (from Barnard, 1959); **h**, *Bullia* (*Bullia*) *tenuis* Reeve, 1846 (4.5 × 2.5 mm) (from Barnard, 1959); **i**, *Bullia* (*Bullia*) *laevissima* (Gmelin, 1791) (5.0 × 3.0 mm) (from Barnard, 1959); **j**, *Bullia* (*Bullia*) *annulata* (Lamarck, 1816a) (10.0 × 8.0 mm) with juvenile specimen (from Barnard, 1959); **k**, *Bullia* (*Bullia*) *callosa* (Wood, 1828) (5.5 × 2.5 mm) (from Barnard, 1959); **l**, *Bullia* (*Cercobullia*) *ceroplasta* (Melvill and Peile, 1924) (from Melvill and and Peile, 1924); **m**, *Bullia* (*Buccinanops*) *cochlidia* (Dillwyn, 1817) (11.0 × 5.0 mm) (MCZM collection, Uruguay); **n**, *Bullia* (*Buccinanops*) *paytensis* (Kiener, 1834) (8.0 × 3.0 mm) (MCZM collection, Uruguay); **o**, *Bullia* ? *granulosa* (Lamarck, 1822) (3.7 × 2.1 mm) (from Adam and Knudsen, 1984); **p**, *Dorsanum miran* (Bruguière, 1789) (3.3 × 2.4 mm) (from Adam and Knudsen, 1984); **q**, *Dorsanum* ? *terebraeforme* (Dautzenberg, 1913) (3.2 × 1.8 mm) (from Adam and Knudsen, 1984); **r**, *Cyllene desnoyersi lamarcki* Cernohorsky, 1975 (5.6 × 2.7 mm) (from Cernohorsky, 1984); **s**, *Nassarius plicatellus* (Adams, 1852) (3.3 × 2.0 mm) (from Adam and Knudsen, 1984; there as *angolensis*); **t–y**, *Nassarius arcularia* (Linnaeus, 1758) variants (from Cernohorsky, 1984).

and *B. duartei* Klappenbach, 1961 (Penchaszadeh, 1971b). In *B. cochlidium* (Dillwyn, 1817) from four to nine embryos may develop and hatch from each capsule (Penchaszadeh, 1973).

In *Dorsanum miran* (Bruguière, 1789), in contrast, egg capsules are apparently always attached to the substrate; each capsule contains numerous developing embryos and the larvae emerge as planktonic veligers (Ansell and Trevallion, 1970, p. 373; Cernohorsky, 1984, p. 23). How long these larvae remain in the plankton and whether they feed there remain unknown.

Shell.—Cossmann (1901b, p. 197) characterized members of the subfamily Dorsaninae as having a slightly twisted columella, a relatively large aperture, and a terminal columellar fold ("*limbe basal*"). This description, however, applies equally well to most other members of Nassariidae. The Recent species of the *Bullia* group are united by the following conchological characters: (1) medium size [compared to the generally smaller size of species of Cylleninae and Nassariinae, and the generally larger size of many species of Buccinidae s. l.]; (2) relatively large body whorl and aperture and a moderate to slightly elongate spire; (3) reduced external sculpture compared to most nassariines; (4) a simple aperture and a simple, short but pronounced anterior canal; and (5) a posterior slit or canal may be present but is seldom well developed or heavily sculptured.

Several authors, including Gray (1839) in his original description, have observed that species of *Bullia* s. s. from South Africa have "a raised band of enamel round the sutures of the whorls, formed by the hinder part of the lip of the shell extending beyond the mouth . . ." (Adams and Adams, 1858, p. 112). Not all South African forms show this feature, however, and most species from the Indian Ocean (*e.g., B. tranquebarica* (Röding, 1798)) do not. Several South American species, on the other hand, do show enamelled sutures. Cernohorsky (1984, p. 23) has suggested that *Buccinanops* is distinguishable from *Bullia* by the presence on the base of the columella of an oblique plait in the former, but some individuals of *Bullia annulata* (Lamarck, 1816a) from South Africa show this feature, as do most specimens of *Dorsanum miran* (Bruguière, 1789) from West Africa. As discussed on p. 10, this character is considered by some authors to be more or less diagnostic of the family Nassariidae as a whole. The most distinct conchological character of *D. miran* is a relatively deep, reflexed dorsal siphonal channel bordered by two distinct oblique spiral ridges (Pl. 1, fig. 15). This contrasts with *Bullia* and *Buccinanops*, both of which have only a single well-marked cord on the adapical posterior margin of the fasciole.

At least some species of South American *Buccinanops* have a periostracum, while South African *Bullia* seem to lack it altogether (Kilburn and Rippey, 1982, p. 97). Cernohorsky (1984, p. 23) states that the periostracum of *Dorsanum* (*Fluviodorsum*) [herein *Bullia*?] *granulosum* (Lamarck, 1822) is thin and finely spirally striate. *D. miran* (Bruguière, 1789) lacks a periostracum (personal observation).

Kilburn and Rippey (1982) and Brown (1982) observe that in many South African *Bullia* species, the shells of females are commonly larger than those of males.

Form of the Shell Apex.—Just as the living species of the *Bullia* group are variable in aspects of their reproductive biology, so also do they appear to be highly variable in the form of the shell apex, a character commonly assumed to be indicative of developmental mode. To summarize in advance, the living species of this group are not consistent in the relationship of protoconch form to reproductive strategy. While it may give some indication, protoconch form alone cannot be taken as conclusive evidence of one or another developmental mode in this group.

The protoconchs of all living species in the *Bullia* group are smooth and unsculptured. Barnard (1959, p. 123) observed that the junction between the protoconch and teleoconch is "not sharply demarkated [*sic*]" in *Bullia* s. s. from South Africa. This seems to apply equally throughout the entire group (see Adam and Knudsen, 1984), and even in well-preserved Recent specimens, the boundaries of the protoconch are often difficult to discern (see Pls. 4–6). The protoconchs of most prosobranchs bear a general relationship to developmental mode. In the broadest terms, species with planktotrophic larvae tend to have smaller protoconchs than those with nonplanktotrophic larvae (Shuto, 1974; Jablonski and Lutz, 1983). Specifically, nonplanktotrophic species have only a protoconch I (P1) and no protoconch II (P2). Planktotrophic species have both P1 and P2. Jablonski and Lutz (1983, p. 31) suggest that egg (= P1) diameters of planktotrophic species range from 0.06 to 0.20 mm, those of nonplanktotrophic species between 0.135 and 0.230 mm, and those of species which brood or encapsulate their larvae between 0.230 and 0.5 mm. Often better results are obtained when the general form of the shell apex is examined from a lateral view. This method more closely follows from the original "apex theory" of Thorson (1950, p. 33) which states that "as a general rule, a clumsy, large apex points to a nonpelagic development, while a narrowly twisted apex, often with delicate sculpture, points to pelagic development."

Protoconch diameters for some Recent species of South African *Bullia* (see Table 2) agree with the theory in being relatively large. Examination of shell apices

Table 2.—Protoconch (P1 + P2) diameters of some living species in the *Bullia* group.

species	diameter		
	Barnard (1959)	*this study**	*Penchaszadeh (1971a)*
Bullia (Bullia) annulata	0.75–1.00	0.7	
Bullia (Bullia) callosa	0.75	0.7	
Bullia (Bullia) digitalis	0.60	0.5	
Bullia (Bullia) diluta	0.75		
Bullia (Bullia) laevissima	0.75	0.5–0.8	
Bullia (Bullia) mozambicensis	0.50		
Bullia (Bullia) natalensis	0.50		
Bullia (Bullia) rhodostoma	0.75	0.5	
Bullia (Bullia) similis	0.3–0.50		
Bullia (Bullia) tenuis	0.8–1.00	1.0	
Bullia (Bullia) trifasciata	1.5		
Dorsanum miran		0.4–0.7	
Bullia (Buccinanops) cochlidia		1.3–2.0	
Bullia (Buccinanops) duartei		0.7–1.0	
Bullia (Buccinanops) globulosa		1.0–1.2	
Bullia (Buccinanops) monilifera		1.2	2.1
Bullia (Buccinanops) uruguayensis		1.8	
Bullia ? granulosa		0.9–1.0	
Bullia ? terebraeformis		0.6	

* All measured specimens are in the MCZ-M collection.

of other species of the *Bullia* group, however, reveals a much more heterogeneous relationship between development and protoconch form.

Plates 4–6 show scanning electron micrographs of the apices of 10 Recent species of the *Bullia* group. Of these species, only *Dorsanum miran* (Bruguière, 1789) [Pl. 6, figs. 5–8] is known to have a planktonic larval stage. Although the protoconch–teleoconch boundary is not conspicuous, its protoconch seems to agree with the theory in being relatively small and multispiral. As already mentioned, it is not known whether the larvae of *D. miran* feed while in the plankton. The protoconchs of several South American species known to release only crawling juveniles also appear to agree with the theory in being relatively large and blunt. The species of *Bullia* s. s. from South Africa, however, show a mixed pattern. *B. callosa* (Wood, 1828) [Pl. 5, figs. 3, 4] and *B. tenuis* Reeve, 1846 [Pl. 5, figs. 5, 6] have relatively large protoconchs, but *B. digitalis* (Dillwyn, 1817) [Pl. 4, figs. 1, 2], *B. laevissima* (Gmelin, 1791) [Pl. 4, figs. 3, 4] and *B. rhodostoma* ? Reeve, 1847 [Pl. 4, figs. 5, 6] show apices more similar to that of *D. miran*. These *Bullia* species are only known to release crawling juveniles. *B. tenuis* shows a blunt apical profile, but those of *B. digitalis* and *B. rhodostoma* are more acute.

The utility of developmental mode (and protoconch form) in taxonomy has been debated. Thorson himself (1950), as well as others (*e.g.*, Robertson, 1974; Turner, Pechenik, and Calloway, 1986) have expressed caution in using this character for species- or genus-level systematics. Cernohorsky (1984, p. 4) states that form of the protoconch is highly variable across the family Nassariidae as a whole and appears not to follow any generic pattern. "It is clear," says Robertson (1974, p. 230), discussing the conclusions of Smith (1945–1946), "that there is no justification for distinguishing genera based exclusively on protoconch differences . . . protoconchs must be evaluated in combination with other characters." Variation in developmental mode within genera appears to be relatively common in prosobranchs (*e.g.* Radwin and Chamberlain, 1973). The genus *Nassarius* Duméril, 1806, for example, includes both planktotrophic and nonplanktotrophic species (Radwin and Chamberlain, 1973; Cernohorsky, 1984).

Thus the relationship of protoconch form and developmental mode is an ambiguous one in the *Bullia* group. Species known to hatch as crawling juveniles show both small and large protoconchs. The single species known to release planktonic veligers shows a relatively small protoconch; it is not known, however, whether this species is planktotrophic or not. Perhaps all species in the group are nonplanktotrophic but variable in protoconch form. Perhaps some species are variable in reproductive mode. The simplicity and lack of sculpture on the early apical whorls of these species make them difficult objects to study. Studies of the larval biology of living species in this group, particularly *Dorsanum miran* (Bruguière, 1789), are necessary to resolve this problem. For the purposes of the present study, especially the question of using protoconch form to infer developmental mode of fossil shells, caution must be used in this group. It may be reasonable to assume that planktotrophic species will have generally smaller protoconchs than nonplanktotrophic species. Nonplanktotrophic species may, however, show a va-

riety of protoconch forms, and a small multispiral protoconch alone cannot be taken as convincing proof of planktonic or planktotrophic habit.

The pattern of sculpture on the early whorls of the teleoconch varies among the living species of the *Bullia* group. In *Buccinanops moniliferum* (Kiener, 1834), the protoconch is commonly followed by two short, relatively inflated whorls bearing pronounced axial costae. This sculpture becomes obsolete within one-quarter of a whorl and the next two or three whorls are more or less smooth, with only traces of axial tubercles on a slightly shouldered adapical ridge. These tubercles become fully developed spines on the sixth and subsequent whorls.

The pattern of axial sculpture is quite different in most South African species of *Bullia* s. s., as well as in *Buccinanops cochlidium* (Dillwyn, 1817) and *B. uruguayensis* (Pilsbry, 1897b) from South America. In these species, faint, low, axial ribs appear on the adapical portion of the first whorl of the teleoconch and are never very pronounced, becoming obsolete on the body whorls of large specimens. *Dorsanum miran* (Bruguière, 1789) shows a variable pattern, in which axial ribs or tubercles may appear on about the fourth or fifth whorl and disappear after no more than two to three whorls. Alternatively the entire teleoconch may be smooth and completely lacking in sculpture (Pl. 1, figs. 14, 16).

SYSTEMATIC SUMMARY[2]

Family **NASSARIIDAE** Iredale, 1916

Genus **BULLIA** Gray *in* Griffith and Pidgeon, 1834

Type Species (by original designation).—*Bullia semiplicata* Gray, 1834 [= *B. callosa* (Wood, 1828)].

Diagnosis.—Development nonplanktotrophic. Lateral radular tooth multicuspidate. Foot very large when expanded, bearing one or two posterior metapodial tentacles. Cephalic tentacles elongate. Eyes absent. Shell bucciniform, small to medium size for shells of this shape. Body whorl usually relatively large and inflated, spire usually, but not always, less than one-half total height; aperture relatively large; anterior canal relatively short, but not retracted. Shell thickness variable. External sculpture usually simple and often absent, consisting when present of spiral grooves and subsutural bands, less often of axial ribs or nodes. Parietal callus slight to moderate. Sculpture inside aperture weak or more often lacking. Outer apertural lip simple and relatively thin. Fasciole usually simple, with a single carina bounding its inner margin and outer lip of anterior canal.

[2] See pp. 100–116, for detailed discussion and justification of the classification presented here.

Subgenus **BULLIA** Gray, 1834[3]

Diagnosis.—Body bears two posterior metapodial tentacles. Shell usually bucciniform, smooth, small to medium-sized for genus; some species have relatively higher spires and moderate sculpture consisting of spiral grooves and/or subsutural shouldering or bands of beaded or spiral ridges. Axial ribbing present on early whorls in some species. Protoconch form and size variable; protoconch–teleoconch boundary gradational. Sutures usually enamelled, but simple in some species. Parietal callus faint to moderately developed, never thick, even when extending onto body whorl. Columella simple, ending in squared or tapering point, less often in a distinct fold. Anterior canal short and narrow but deep. Anterior notch bordered adaperturally by single carina, which extends around columella to callus. Fasciole anterior to carina simple, usually bearing spiral ridges and/or sigmoidal growth lines.

Remarks.—Melvill and Peile (1924) proposed the genus name *Cereobullia* for *Bullia ceroplasta* Melvill, 1898, stating that this species differs from other *Bullia* species "by its waxen appearance and the smooth, proportionately wide, longitudinal ribs," and also in features of the radula and operculum (Pl. 1, fig. 13; Textfigs. 3, 4). Cernohorsky (1984) recognized *Cereobullia* as a subgenus of *Bullia*. Based on published information on radular differences, as well as examination of a specimen of *B. ceroplasta* in the USNM collections, I agree that it is morphologically distinct. It is similar to some *Bullia* s. s. species in its relatively high spire and to almost all of these species in its lack of a terminal columellar fold. It is considerably smaller than almost all other *Bullia* species, however, and no other species has pronounced axial ribs extending over the entire surface of the shell. I have not examined sufficient material to resolve the taxonomic status of this species, and in the phylogenetic analysis presented on pp. 100–108 it is included in the genus *Bullia*.

The species of *Bullia* (*Bullia*) form a variable but coherent morphological and ecological entity in the shallow water faunas of the southern African coast and the western and northern Indian Ocean. It is possible that a detailed phylogenetic analysis of these species using data from both shell morphology and soft part anatomy would suggest that the group should be subdivided. Several species from the northwestern Indian Ocean, in particular, are divergent from most South African species. Mörch's (1852) concept of the genus *Pseudostrombus* seems to have reflected this idea, including as it did several of the high-spired, more sculptured Indian Ocean species [*e.g.*, *B. tranquebarica* (Röding, 1798), *B. vittata* (Linnaeus, 1767)].

[3] = *Leiodomus* Swainson, 1840; *Bulliana* Gray, 1850; *Pseudostrombus* Mörch, 1852; ? *Cereobullia* Melvill and Peile, 1924.

The Recent species of *Bullia* recognized as valid by Cernohorsky (1984) are listed in Table 3a. Some of these (*e.g., Bullia* (*Bullia*) *trifasciata* Smith, 1904 [Pl. 2, fig. 10]) are illustrated in Plate 2.

Subgenus **BUCCINANOPS** d'Orbigny, 1841

Type Species (by original designation).—*Buccinum globulosum* Kiener, 1834.

Diagnosis.—Body bears single posterior metapodial tentacle. Shell bucciniform, usually thick and robust in appearance. Spire never greater than one-third shell height. Columella bears pronounced terminal fold. Internal sculpture almost always lacking. External sculpture usually simple, only one species showing elements other than faint spiral grooves and slight subsutural shouldering on late whorls. At least one species has a thin, dark periostracum. Parietal callus usually expanded onto body whorl but never thick. Anterior canal relatively wide and elongate. Sutures often enamelled, but not as conspicuously as in *Bullia* s. s.

Remarks.—In his original description of this taxon, d'Orbigny (1841, p. 434) apparently considered aspects of both Old and New World taxa, listing attributes that describe not only the South American species discussed here under *Bullia* (*Buccinanops*), but also South African and Indian Ocean species discussed above under *Bullia* (*Bullia*).

New descriptions of the shells of all living species of *Buccinanops*, based on examinations of large series in three museum collections, are presented below.

Bullia (Buccinanops) globulosa (Kiener)
Plate 2, figure 14

Buccinum globulosum Kiener, 1834, p. 12, pl. 10, fig. 33.
Buccinanops globulosum (Kiener). d'Orbigny, 1841, p. 157; d'Orbigny, 1845, p. 198; d'Orbigny, 1846, p. 435, pl. 61, fig. 24; Gray, 1854, p. 40; Carcelles and Parodiz, 1939, pp. 764ff, figs. 7–9; Carcelles, 1950, p. 63; Barattini and Ureta, 1960, p. 117.
Bullia globulosa (Kiener). Reeve, 1846, species 5, pl. 1, fig. 5; Adams and Adams, 1858, p. 116; Kobelt, 1877, p. 290; Tryon, 1882, p. 11, pl. 5, fig. 60; Pilsbry, 1897b, p. 6; Ameghino, 1906, p. 279; Ihering, 1907, p. 405; Frenguelli, 1930, p. 36; Frenguelli, 1931, pp. 11, 26, 28; Feruglio, 1933, pp. 36ff, pl. 8, figs. 16a, b; Abbott and Dance, 1983, p. 178.
Bullia (*Buccinanops*) *globulosum* (Kiener). Paetel, 1888, p. 116.
Buccinanops globulosum var. *elata* Strebel, 1906, p. 151, pl. 11, figs. 75a, b.

Occurrence.—Uruguay and Patagonia to Tierra del Fuego.

Material examined.—MCZ(M) 109788 (Puerto Madryn, Chubut, Argentina), 296191 (Puerto San Antonio, Patagonia), 296192 (Puerto San Antonio, Patagonia), 296193 (Río Negro, Patagonia), 296194 (Puerto San Antonio, Patagonia); USNM 338396 (Río Negro, Patagonia); ANSP 34595 (Río Negro, Patagonia), 70704 (Maldonado Bay, Uruguay), 78081 (Cape Fairweather, Patagonia), 88524 (mouth of Santa Crúz River, Argentina), 103324 (Punta Arenas, Chile), 170447 (Puerto Madryn, Chubut, Argentina), 178643 (Golfo San Jorge, Patagonia), 236042 (Comodoro Rivadavia, Argentina), 285623 (Punta del Este, Maldonado Bay, Uruguay), 312315 (Rawson, Chubut, Argentina), 312327, 316684 (Comodoro Rivadavia, Patagonia), 338396 (Río Negro, Patagonia) [total: 84 specimens].

Description.—Small to moderate size, not exceeding 30 mm total height. Very similar to *Bullia* (*Bullia*) *laevissima* (Gmelin, 1791) from South Africa. Spire very short, comprising less than one-fifth total height. Protoconch unknown. Body whorl shouldered, inflated, straight-sided. Aperture relatively large, showing a slight posterior sinus. Sutures often enameled. Fasciole variable but generally simple; columella showing a well-marked terminal fold. External shell sculpture lacking. Color tan-brown, with lighter areas at shoulders and sutures.

Bullia (Buccinanops) cochlidia (Dillwyn)
Plate 3, figures 1–13; Plate 6, figures 3, 4

? *Buccinum labyrinthus* Gmelin, 1791, p. 3486.
Buccinum cochlidium Chemnitz *in* Martini and Chemnitz, 1795, p. 275, pl. 209, figs. 2053, 2054; Dillwyn, 1817, p. 627; Kiener, 1834, p. 10, pl. 16, fig. 17; Anton, 1838, p. 91; Deshayes, 1844, pp. 187–188; Martens, 1872, p. 25.
Buccinum Lamarckii Kiener, 1834, p. 5. pl. 3, fig. 6.
Buccinanops cochlidium (Dillwyn). d'Orbigny, 1841, p. 157; d'Or-

Table 3a.—Recent and fossil nassariid species included in the *Bullia* group. Genera are listed alphabetically; species are listed alphabetically within genera or subgenera. Recent species of *Bullia* (*Bullia*) are from Cernohorsky (1984). Species of *Buccinopsis* are mainly from Sohl (1964) and Jablonski (1979). All other taxa discussed in more detail in the text. Not listed are the species from the Tertiary of the Ukraine and eastern Europe assigned to *Dorsanum* by Zelinskaya *et al.* (1968). These are listed in Table 12a. Also not included are species from the Tertiary of Japan asssigned to "*Molopophorus*" (see Masuda and Noda, 1976; Oyama, Mizuno, and Sakamoto, 1960).

taxon	*age*	*distribution*
"*Adinopsis*" *skoogi* Odhner, 1923	Recent[a]	West Africa
Buccinopsis crassa (Wade, 1917)	Upper Cretaceous	TN, TX
Buccinopsis crassicostata (Gabb, 1876)	Upper Cretaceous	GA
Buccinopsis dorothiella Sohl, 1964	Upper Cretaceous	GA, MS
Buccinopsis globosus (Gabb, 1876)	Upper Cretaceous	NJ–NC
Buccinopsis greenensis (Stephenson, 1923)	Upper Cretaceous	NC

Table 3a.—Continued.

taxon	*age*	*distribution*
Buccinopsis parryi (Conrad, 1857)	Upper Cretaceous	TX
Buccinopsis solida (Wade, 1917)	Upper Cretaceous	MS, TN
Buccinopsis solida solida (Wade, 1917) of Sohl, 1964	Upper Cretaceous	MS, TN
Bullia (*Bullia*) *aikeni* Kilburn, 1978	Recent*	East Africa
Bullia (*Bullia*) *ancillaeformis* Smith, 1906	Recent*	South Africa
Bullia (*Bullia*) *annulata* (Lamarck, 1816a)	Plio-Pleistocene–Recent	South Africa
Bullia (*Bullia*) *callosa* (Wood, 1828)	Plio-Pleistocene–Recent	South Africa
Bullia (*Bullia*) *cataphracta* Kilburn, 1978	Recent*	East Africa
Bullia (*Bullia*) *cumingiana* Dunker, 1852	Recent*	Persian Gulf
Bullia (*Bullia*) *digitalis* (Dillwyn, 1817)	Plio-Pleistocene–Recent	South Africa
Bullia (*Bullia*) *diluta* (Krauss, 1848)	Plio-Pleistocene–Recent	South Africa
Bullia (*Bullia*) ? *granulosa* (Lamarck, 1822)	Recent*	West Africa
Bullia (*Bullia*) ? *gruveli* (Dautzenberg, 1910)	Recent*	West Africa
Bullia (*Bullia*) *indusindica* Melvill, 1898	Recent*	Pakistan
Bullia (*Bullia*) *kurrachensis* Angas, 1877	Recent*	India
Bullia (*Bullia*) *laevissima* (Gmelin, 1791)	Plio-Pleistocene–Recent	South Africa
Bullia (*Bullia*) *mauritiana* Gray, 1839	Recent*	Madagascar?
Bullia (*Bullia*) *melanoides* (Deshayes, 1832)	Recent*	Persian Gulf
Bullia (*Bullia*) *mozambicensis* Smith, 1878	Plio-Pleistocene–Recent	East Africa
Bullia (*Bullia*) *natalensis* (Krauss, 1848)	Plio-Pleistocene–Recent	South Africa
Bullia (*Bullia*) *nitida* Sowerby, 1895	Recent*	Persian Gulf
Bullia (*Bullia*) *nuttalli* Kilburn, 1978	Recent*	East Africa
Bullia (*Bullia*) *osculata* Sowerby, 1900	Recent*	South Africa
Bullia (*Bullia*) *othaeitensis* (Bruguière, 1789)	Recent*	Indo-Pacific?
Bullia (*Bullia*) *persica* Smith, 1878	Recent*	Persian Gulf
Bullia (*Bullia*) *pura* Melvill, 1885	Plio-Pleistocene–Recent	South Africa
Bullia (*Bullia*) *rhodostoma* Reeve, 1847	Recent*	South Africa
Bullia (*Bullia*) *rogersi* Smythe and Chatfield, 1981	Recent*	Gulf of Oman
Bullia (*Bullia*) *sendersi* Kilburn, 1978	Recent*	East Africa
Bullia (*Bullia*) *similis* Sowerby, 1897	Plio-Pleistocene–Recent	South Africa
Bullia (*Bullia*) *tenuis* Reeve, 1846	Plio-Pleistocene–Recent	South Africa
Bullia (*Bullia*)? *terebraeformis* (Dautzenberg, 1913)	Recent*	West Africa
Bullia (*Bullia*) *townsendi* Melvill, 1912	Recent*	Gulf of Oman
Bullia (*Bullia*) *tranquebarica* (Röding, 1798)	Recent*	India
Bullia (*Bullia*) *trifasciata* Smith, 1904	Recent*	South Africa
Bullia (*Bullia*) *turrita* Gray, 1839	Recent*	(?)
Bullia (*Bullia*) ? *valida* Dunker, 1852	Recent*	(?)
Bullia (*Bullia*) *vittata* (Linnaeus, 1767)	Recent*	East Africa
Bullia (*Buccinanops*) ? *clarki* Wagner and Schilling, 1923	middle–upper Oligocene	CA
Bullia (*Buccinanops*) *cochlidia* (Dillwyn, 1817)	Plio-Pleistocene–Recent	South America
Bullia (*Buccinanops*) *deforme* (King and Broderip, 1831)	Plio-Pleistocene–Recent	South America
Bullia (*Buccinanops*) *duartei* (Klappenbach, 1961)	Recent*	South America
Bullia (*Buccinanops*) *fuegina* (Steinmann and Wilckens, 1908)	lower Miocene	South America
Bullia (*Buccinanops*) *globulosa* (Kiener, 1834)	Plio-Pleistocene–Recent	South America
Bullia (*Buccinanops*) *monilifera* (Kiener, 1834)	Recent*	South America
Bullia (*Buccinanops*) *nordenskjoldi* (Steinmann and Wilckens, 1908)	lower Miocene	South America
Bullia (*Buccinanops*) *paytensis* (Kiener, 1834)	Recent*	South America
Bullia (*Buccinanops*) *uruguayensis* Pilsbry, 1897b	Plio-Pleistocene–Recent	South America
Bullia (*Bulliopsis*) *choctavensis* (Aldrich, 1886)	upper Paleocene–middle Eocene	AL
Bullia (*Bulliopsis*) *integra* (Conrad, 1842)	middle Miocene	MD
Bullia (*Bulliopsis*) *marylandica* Conrad, 1862a	middle Miocene	MD
Bullia (*Bulliopsis*) *quadrata* (Conrad, 1830)	middle–upper Miocene	MD, VA
Bullia (*Bulliopsis*) *quadrata bowlerensis*, n. subsp.	upper Miocene	VA
Bullia (*Bulliopsis*) *variabilis* (Whitfield, 1894)	lower–middle Miocene	NJ
Bullia (*Cereobullia*) *ceroplasta* (Melvill and Peile, 1924)	Recent*	Indian Ocean
Calophos baranoanus (Anderson, 1929)	middle Miocene	Colombia, Venezuela
Calophos bombax (Olsson, 1964)	upper Miocene–lower Pliocene	Ecuador
Calophos ectyphus Woodring, 1964	middle Miocene	Panama
Calophos (?) *esmereldensis* (Olsson, 1964)	upper Miocene–lower Pliocene	Ecuador, Venezuela
Calophos golfoyaquensis (Maury, 1917)	Miocene	Dominican Republic
Calophos inornata (Gabb, 1881)	lower Miocene	Costa Rica
Calophos mixteca (Perrilliat Montoya, 1963)	middle Miocene	Mexico

Table 3a.—Continued.

taxon	*age*	*distribution*
Calophos oldroydae (Dall and Ochsner, 1928)	upper Pliocene	Galapagos
Calophos plicatilis (Böse, 1906)	middle Miocene	FL (?), Mexico
Calophos rohri (Rutsch, 1942)	upper Miocene–lower Pliocene	Trinidad
Calophos tropicalis (Dall and Ochsner, 1928)	upper Pliocene	Galapagos
Calophos ursus (Olsson, 1964)	middle Miocene	Ecuador
Calophos wilsoni, n. sp.	upper Pliocene	FL
Calophos ? zorritensis (Nelson, 1870)	upper Miocene	Peru
Colwellia antiquata (Gabb, 1864)	middle Eocene	CA
Colwellia auversiensis (Deshayes, 1865)	Eocene	France
Colwellia bretzi (Weaver, 1912)	upper Eocene	WA
Colwellia cretacea (Gabb, 1864)	middle Eocene	CA
Colwellia flexuosa (Edwards, 1866)	Eocene	UK
Colwellia tejonensis (Dickerson, 1915)	upper Eocene	CA, WA
"*Cyllenina*" *aequistriata* Dollfus, 1889	upper Miocene	France
"*Cyllenina*" *angusta* (Hölzl, 1958)	Miocene ?	Austria, Germany
"*Cyllenina*" *baccata* (Basterot, 1825)	lower Miocene	France
"*Cyllenina*" *deshayesi* (Mayer, 1862)	Miocene ?	Germany
"*Cyllenina*" *gradata* Peyrot, 1925–1926	lower Miocene	France
"*Cyllenina*" *haueri* (Michelotti, 1847)	lower Miocene	Germany
"*Cyllenina*" *hungarica* (Gábor, 1936)	upper Oligocene	central Europe
"*Cyllenina*" *intermedia* (Hölzl, 1958)	upper Miocene	Germany
"*Cyllenina*" *nodosocostata* (Hilber, 1879)	Miocene	Germany
"*Cyllenina*" *plicata* (Grateloup, 1834)	lower–middle Miocene	France
"*Cyllenina*" *ruida* Peyrot, 1925–1926	lower Miocene	France
"*Cyllenina*" *sturi* (Hoernes and Auinger, 1882)	Miocene	Germany
"*Cyllenina*" *subpolita* (d'Orbigny, 1852)	lower–upper Miocene	France
Desorinassa acies (Watelet, 1853)	Eocene	France
Desorinassa ? bonnecarrei (Furon *in* Furon and Kouriatchy, 1948)	lower Eocene	Togo
Desorinassa desori (Deshayes, 1865)	Paleocene	France, UK
Desorinassa lata (Deshayes, 1865)	Paleocene	France
Desorinassa ovata (Deshayes, 1835)	Eocene	France
Desorinassa ? supracostata (Traub, 1938)	Paleocene	Austria
Desorinassa williamsi Nuttall and Cooper, 1973	Paleocene	UK
Dorsanum miran (Bruguière, 1789)	Recent*	West Africa
"*Dorsanum*" *lagunitense* (Woods, 1922)	lower Eocene	Peru
"*Dorsanum*" *parinense* (Olsson, 1928)	middle Eocene	Peru
Keepingia annandalei (Vredenburg, 1925)	Oligocene	Germany
Keepingia aturensis (Peyrot, 1927)	lower Miocene	France
Keepingia bolli (Beyrich, 1854)	Oligocene	Germany
Keepingia cassidaria (Sandberger, 1863)	Oligocene	Germany
Keepingia gossardi (Nyst, 1836)	Oligocene	Belgium, France
Keepingia praecedens (Peyrot, 1927)	lower Miocene	France
Keepingia tarbellica (Grateloup, 1834)	lower Miocene	France
Keepingia uniseriale (Sandberger, 1863)	Oligocene	Germany
"*Molopophorus*" *anglonanus* (Anderson, 1905)	lower–middle Miocene	CA, OR, WA
"*Molopophorus*" *biplicatus* (Gabb, 1866)	middle Oligocene–lower Miocene	CA, WA
"*Molopophorus*" *bogachielii* (Reagan, 1909)	upper Miocene	AK, OR, WA, BC
"*Molopophorus*" *dalli* Anderson and Martin, 1914	lower–middle Oligocene	CA, OR
"*Molopophorus*" *gabbi* Dall, 1909	lower–middle Oligocene	CA, OR, WA
"*Molopophorus*" *lincolnensis* Weaver, 1916	upper Eocene–lower Miocene	WA
"*Molopophorus*" *matthewi* Etherington, 1931	lower–middle Miocene	AK, WA
"*Molopophorus*" *newcombei* (Merriam, 1897)	upper Oligocene–lower Miocene	BC
"*Nassa*" *veneris* Faujas de Saint-Fond, 1817	lower Miocene	France
Pseudocominella armata (Sowerby, 1850)	Eocene	UK
Pseudocominella bullata (Philippi, 1847)	Oligocene	Germany
Pseudocominella deserta (Solander, 1766)	Eocene	UK
Pseudocominella semicostata Nuttall and Cooper, 1973	Eocene	UK
Pseudocominella solanderi (Cossmann, 1889)	Eocene	UK
Thanetinassa bicorona (Melleville, 1843)	Paleocene	France
Whitecliffia suturosa (Nyst, 1836)	Oligocene	Belgium
Whitecliffia tumida Nuttall and Cooper, 1973	Eocene	UK

* Recent species that lack a known fossil record.

Table 3b.—Fossil nassariid species excluded from the *Bullia* group.

taxon	*age*	*distribution*
Adinus truncatus (Reeve, 1846)	Recent*	unknown
Ancillopsis patula (Deshayes, 1835)	Eocene	France
?*Austrocominella cepa* (Sowerby, 1846)	Tertiary	Chile
?*Austrocominella fuegensis* (Ihering, 1907)	lower Miocene?	Tierra del Fuego
?*Austrocominella iheringi* Feruglio, 1936	Tertiary	Argentina
?*Austrocominella obesa* (Philippi, 1887)	Tertiary	Chile
?*Austrocominella opima* (Philippi, 1887)	Tertiary	Chile
?*Austrocominella patagonica* Feruglio, 1936	Tertiary	Argentina
?*Austrocominella polypleura* (Philippi, 1887)	Tertiary	Chile
?*Austrocominella retusa* (Philippi, 1887)	Cretaceous	Chile
Brachysphingus gabbi Stewart, 1927	Paleocene	CA
Brachysphingus gibbosus Nelson, 1925	Eocene	CA
Brachysphingus mammilatus Clark and Woodford, 1927	Eocene	CA
Brachysphingus sinuatus Gabb, 1869	Paleocene	CA
"*Buccinanops*" *ellipticum* (Whitfield, 1865)	upper Paleocene–middle Oligocene?	AL, MS, TX
"*Bullia*" *altilis* (Conrad, 1832b)	Paleocene–Eocene	AL, LA, MS, TX
"*Bullia*" *ancillops* (Heilprin, 1891)	lower–middle Eocene	TX
"*Bullia*" *calluspira* (Dockery, 1980)	middle Eocene	MS
"*Bullia*" *scamba* (Conrad, 1832b)	middle Eocene	AL
"*Bullia*" *tenera* (Conrad, 1834)	middle Eocene	AL, TX
"*Bullia*" *tuomeyi* (Aldrich, 1921)	upper Paleocene	AL
Bulovia weisbordi Palmer, 1937	middle Eocene	TX
"*Dorsanum*" *bellaliratum* (Gabb, 1862)	middle Eocene	AL
"*Dorsanum*" *scalatum* (Heilprin, 1891)	middle Eocene	TX
Lisbonia expansa (Aldrich, 1886)	middle Eocene	AL
"*Melanopsis*" *anita* (Aldrich, 1886)	upper Paleocene	AL
"*Molopophorus*" *aequicostatus* Vokes, 1939	middle Eocene	CA
"*Molopophorus*" *bramkampi* Clark and Anderson, 1938	lower Oligocene	CA
"*Molopophorus*" *californicus* Clark and Woodford, 1927	Paleocene–middle Eocene	CA, OR
"*Molopophorus*" *clarki* (Weaver, 1912)	upper Eocene	WA
"*Molopophorus*" *crooki* Clark, 1938	upper Eocene	CA
"*Molopophorus*" *effingeri* Weaver, 1942	lower Oligocene	WA
"*Molopophorus*" *fishii* (Gabb, 1869)	middle–upper Oligocene	CA, OR, BC
"*Molopophorus*" *stephensoni* Dickerson, 1917	lower Oligocene	CA, WA
"*Molopophorus*" *striatus* (Gabb, 1869)	upper Eocene	CA
Monoptygma crassiplicum Conrad *in* Gabb, 1860	middle Eocene	TX
Monoptygma curtum Conrad, 1865a	middle Eocene	TX
Monoptygma leai Whitfield, 1865	middle Eocene	AL
Monoptygma lymneoides (Conrad, 1833b)	middle Eocene	AL
"*Perunassa*" *ecuadorensis* (Pilsbry and Olsson, 1941)	lower Pliocene	Peru
Pseudoliva spp.	Tertiary–Recent	cosmopolitan

? Taxa probably but not definitely excluded from the *Bullia* group.
* Recent species that lack a known fossil record.

bigny, 1845, p. 199; d'Orbigny, 1846, p. 434; Gray, 1850, p. 20, 139, pl. 98, fig. 9; Cossmann, 1901b, p. 220; Carcelles and Parodiz, 1939, pp. 751–754, fig. 6; Carcelles, 1944, p. 250; Barattini and Ureta, 1960, pp. 113–114; Cernohorsky, 1984, p. 27.

Buccinum gradatum Deshayes, 1844, pp. 186–187.

Bullia gradata (Deshayes). Reeve, 1846, species 3, pl. 4, fig. 4; Abbott and Dance, 1983, p. 177.

Bullia cochlidium Chemnitz. Wood and Hanley, 1856, p. 117, pl. 23, fig. 95; Chenu, 1859, p. 159, fig. 747; Kobelt, 1877, p. 288.

Bullia (*Buccianops*) [*sic*] *cochlidium* Kiener. Adams and Adams, 1858, p. 113.

Bullia (*Buccianops*) [*sic*] *gradata* Deshayes. Adams and Adams, 1858, p. 113.

Bullia (*Buccinanops*) *gradatum* Deshayes. Chenu, 1859, p. 160, fig. 751.

Bullia Lamarckii (Kiener). Kobelt, 1877, p. 288.

Bullia (*Buccinanops*) *cochlidium* (Dillwyn). Tryon, 1882, p. 13, pl. 5, fig. 73, pl. 6, figs. 76–81; Paetel, 1888, p. 116; Dall, 1893, p. 111; Thiele, 1929, p. 32; Cernohorsky, 1982, p. 17-238, fig. 17-827.

? *Bullia labyrinthum* (Gmelin). Tryon, 1882, p. 13, pl. 6, fig. 95.

Buccinanops (*Buccinanops*) *cochlidium* (Kiener). Fischer, 1884, p. 636.

Bullia gradata pampeana Ihering, 1907, p. 422, 425.

Buccinanops gradatum (Deshayes). Carcelles and Parodiz, 1939, pp. 754–758, figs. 3–5; Carcelles, 1944, p. 250; Barattini and Ureta, 1960, p. 114; Rios, 1970, p. 93, pl. 27; Cernohorsky, 1984, p. 28.

Buccinanops lamarckii (Kiener). Rios, 1970, p. 93; Rios, 1975, p. 96, pl. 27, fig. 401.

Occurrence.—Southern Brazil to Tierra del Fuego.

Material examined.—MCZ(M) 109343 (Monte Hermosa, Argentina), 109426 (Puerto San Antonio, Pa-

tagonia), 118668 (Buenos Aires, Argentina), 198294 (Puerto Lobos, Patagonia), 198430 (San Antonio, Río Negro, Patagonia), 198446 (Buenos Aires), 201331 (Punta del Este, Uruguay), 219076 (Punta del Este, Uruguay), 296181 (no locality given), 296182 (no locality given), 296183 (Puerto San Antonio, Patagonia), 296184 (no locality given), 296185 (Cassino Beach, Patagonia), 296186 (Patagonia), 296187 (Patagonia), 296188 (no locality given), 296189 (Rio Grande do Sul, Brazil), 296190 (Brazil); USNM 16818 (Río Negro, Patagonia), 60073 (Straits of Magellan), 125500 (Rio Grande do Sul, Brazil), 170215 (Río de La Plata, Patagonia), 185359 (Uruguay), 219862 (Monte Hermosa, Argentina), (?) 224496 (Río de La Plata, Patagonia), 270862 (near Montevideo, Uruguay [Pleistocene]), 270865, 331316 (Cabo Santa Maria, Uruguay), 349194 (Cape Polonia, Uruguay), 349185 (Buenos Aires, Argentina), 359232 (Piriapolis, Uruguay), 359243 (Lobos Island, Uruguay), 359259 (Coronilla Island, Rocha, Uruguay), 415887 (southeast South America), 463581 (Monte Hermosa, Argentina), 654362 (Rio Grande, Rio Grande do Sul, Brazil), 807977 (Saco de Mangueriera, Rio Grande do Sul, Brazil); ANSP 34616, 34617 (South America), 34618 (no locality given), 34719 (Río Negro, Patagonia), 60140 (Brazil), 70506 (Maldonado, Uruguay), 142678 (South America), 195121 (Rio Grande do Sul, Brazil), 236021 (Cabo San Antonio, Argentina), 236043 (Golfo San Matias, Argentina), 244148, 249092 (Ilha Grande, Rio State, Brazil), 251783 (Punta Ballena, near Maldonado, Uruguay), 253107 (La Paloma, Rocha, Uruguay), 285622 (Punta del Este, Maldonado, Uruguay), 312317 (Rawson, Chubut, Argentina), 314863 (La Paloma, Rocha, Uruguay), 337666 (Río Nigre, Chile ?) [total: 127 specimens].

Description.—Large for subgenus, up to 100 mm total height, more commonly less than 70 mm. Shell fusiform to bucciniform. Protoconch large, paucispiral (one to two whorls, diameter approximately 1.2 mm). Spire height one-third to one-fourth total height. Body whorl relatively large, often inflated. Aperture relatively large, usually approximately one-half total height, occasionally more. Whorls may bear pronounced subsutural shoulder or carina, a slight shoulder, or may meet the suture smoothly. Sutures may or may not be enamelled, but never heavily so. Callus slight to moderate in thickness and extent over body whorl. Shell normally unsculptured and smooth, except for infrequent axial ribs (approximately 15 per whorl) on first three to four teleoconch whorls of some specimens. Growth lines occasionally pronounced on body whorl of large specimens. Terminal columellar fold pronounced. Anterior canal relatively wide and deep. Shell usually thick and heavy but may be thin to translucent. Periostracum thin, dark brown. Shell white to pale tan, occasionally with irregular longitudinal light-brown striping.

Remarks.—Deshayes (1844) observed that *Buccinum cochlidium* of Kiener, 1834 differed in a number of respects from *B. cochlidium* Chemnitz *in* Martini and Chemnitz, 1795. The angle between the subsutural shelf and the side of the whorls in the former was acute, he said, while that of the latter was generally obtuse. He added that *B. cochlidium* of Kiener had a prominent callus, while *B. cochlidium* of Chemnitz lacked a callus. Deshayes therefore introduced the name *Buccinum gradatum* for Kiener's *B. cochlidium.*

Tryon (1882, p. 13) disputed this separation, writing, "I do not agree with Deshayes and Reeve [1846] that Kiener's species is different from that of Chemnitz, ... The fact is that *B. cochlidium* is of rude, frequently distorted growth, and a collection of specimens exhibits many forms." Under *Bullia cochlidia*, Tryon synonymized *B. gradata* Deshayes, 1844, *B. lamarckii* Kiener, 1834, *B. paytense* Kiener, 1834, *B. squalida* King and Broderip, 1831, and *B. labyrinthum* (Gmelin, 1791), describing the last as a "remarkably distorted shell." *Bullia annulata* (Lamarck, 1816a) [from South Africa], added Tryon, "may be only a variety of *cochlidium*, while *B. armata* Gray, 1839 [= *monilifera* (Kiener, 1834)] was considered by d'Orbigny merely a spinose variety of *B. cochlidium*" (Tryon, 1882, p. 14).

Carcelles and Parodiz (1939) maintained *cochlidium* Dillwyn, 1817 and *gradatum* Deshayes, 1844 as distinct species, but did not present much specific evidence for this judgement. They noted that the anterior canal is always wider in *gradatum* than in *cochlidium*, though the shape and extent of the callus is approximately the same in the two forms (contra Deshayes, cited above), and that the inner lip of the aperture is more concave in *gradatum* than *cochlidium.* They described the radula of *gradatum* as having rachidian plates of eight teeth, more pointed in juveniles than in adults, and laterals with a variable number of cuspids according to the size and age of the animal; no radular information was provided for *cochlidium.* Text-figures 3g and 3i show that even among individuals identified as *gradatum* there may be variability in radular form.

While the photographs provided by Carcelles and Parodiz show differences between adult individuals considered representative of *gradatum* and *cochlidium*, the authors stated that juvenile *cochlidium* often have less inflated body whorls than adults, making them resemble adult *gradatum.* Adult *gradatum*, they concluded, however, show great variability, from a very inflated to a less inflated, elongate form. This variation, they added, does not seem to be sufficiently regular to allow the designation of subspecies.

"Typical" *gradatum* differs from "typical" *cochlidium* in having a pronounced subsutural shoulder or carina, and in having a much thicker, wider callus. In extreme individuals these conchological differences would seem to justify specific separation. Consideration of the entire range of morphologic and geographic variation, however, suggests that an almost continuous spectrum of form is present, from highly carinate or shouldered, to well-rounded. Samples from single localities show virtually the same pattern as the total sample; the smooth and shouldered morphs are not segregated geographically. Until species-level differences can be demonstrated in anatomical characters or reproductive behavior, it is reasonable to consider *cochlidium* and *gradatum* to be morphological extremes of a single, variable species. This conclusion has also been favored recently by Cernohorsky (1984) and Abbott and Dance (1983), among others.

Bullia (Buccinanops) paytensis (Kiener)
Plate 2, figure 9

Buccinum squalidum King and Broderip, 1831[4], p. 349 [*non* Gmelin, 1791].
Buccinum Paytense Kiener, 1834, p. 17, pl. 6, fig. 16.
Buccinum citrinum Reeve, 1846, pl. 9, species 70; Strebel, 1906, p. 153, pl. 11, figs. 74a, b.
Buccinum squalida King. Reeve, 1846, species 26, pl. 4, fig. 26; Adams and Adams, 1858, p. 113; Cunningham, 1870, p. 476; Kobelt, 1877, p. 289; Smith, 1905, p. 334.
Bullia (*Buccinanops*) *squalida* (King). Paetel, 1888, p. 117.
Buccinanops squalidus (King). Carcelles, 1950, p. 62, pl. 2, fig. 40.
Bullia (*Buccinanops*) *paytensis* (Kiener). Cernohorsky, 1982, p. 17-239.
Buccinanops paytense (Kiener). Cernohorsky, 1984, p. 30.

Occurrence.—Patagonia and Tierra del Fuego to Chile and Peru.

Material examined.—MCZ(M) 118667 (Playa del Río del Fuego, Tierra del Fuego), 149244 (Golfo de San Jorge, Chubut, Patagonia) 198451 (Cabo Buen Tiempo, Gallegos, Patagonia), 198440 (San Gregorio, Straits of Magellan), 296198 (Comodoro Rivadavia Territory, Argentina), 296199 (Paraca Bay, Peru), 296201 (Paraca Bay, Peru), 296202 (Straits of Magellan), 296203 (no locality given); USNM 102533 (Gregory Bay, Straits of Magellan), (?) 102585 (Patagonia), 126896 (Tierra del Fuego), (?) 217107 (Maldonado, Uruguay), (?) 340683 (Cabo Santa Maria, Rocha, Uruguay), (?) 340684 (Maldonado, Uruguay), 360446 (Comodoro Rivadavia, Argentina) [total: 108 specimens].

Description.—Bucciniform, of moderate size for subgenus, not exceeding 50–55 mm total height. Protoconch unknown. Spire relatively high, but lower-spired than *cochlidia* (Dillwyn, 1817). Body whorl gently rounded, without subsutural shouldering. Parietal callus noticeable but thin. Terminal columellar fold pronounced; columella otherwise simple and smooth. Aperture lacking posterior sinus or slit. Anterior canal of moderate length. Sutures occasionally enameled, but more often simple. External sculpture usually absent, but some specimens bear subsutural spiral grooves, rarely covering the entire body whorl. Color pattern variable. Most pale tan, white or pinkish.

Remarks.—*Buccinum squalidum* King and Broderip, 1831 is a primary homonym of *Buccinum squalidum* Gmelin, 1791. The name *paytensis* is the next available name for this species.

Bullia (Buccinanops) monilifera (Kiener)
Plate 2, figure 12; Plate 6, figures 1, 2

Buccinum moniliferum Valenciennes[5]. Kiener, 1834, p. 11, pl. 3, fig. 8; Anton, 1838, p. 91; Deshayes, 1844, p. 191; d'Orbigny, 1845, p. 199.
Bullia armata Gray, 1839, p. 126; Reeve, 1846, species 2, pl. 1, fig. 2; Kobelt, 1877, p. 290.
Buccinum (*Buccinanops*) *moniliferum* d'Orbigny, 1846, p. 434.
Bullia (*Buccianops*) [*sic*] *armata* Gray. Adams and Adams, 1853, p. 113.
Buccinanops cochlidium (Dillwyn) (var. 3, with tubercular band or suture) Gray, 1854, p. 41 [*non cochlidium* Chemnitz *in* Martini and Chemnitz, 1795, *nec* Dillwyn, 1817, *nec* Kiener, 1834].
Bullia (*Buccinanops*) *moniliferum* Valenciennes. Chenu, 1859, p. 160, fig. 750.
Bullia (*Buccinanops*) *armata* Gray. Tryon, 1882, p. 14, pl. 16, figs. 82, 83; Paetel, 1888, p. 116.
Dorsanum armatum (Gray). Cossmann, 1901b, p. 218.
Dorsanum moniliferum (Kiener). Carcelles and Parodiz, 1939, pp. 747ff, figs. 1,2; Carcelles, 1944, pp. 249–250, Barattini and Ureta, 1960, p. 113; Rios, 1970, p. 92, pl. 28; Rios, 1975, pp. 95–96, pl. 27, fig. 398.
Bullia (*Dorsanum*) *monilifera* (Kiener). Cernohorsky, 1982, p. 17-239, fig. 17-871.
Bullia monilifera (Kiener). Abbott and Dance, 1983, p. 177.
Buccinanops moniliferum (Kiener). Cernohorsky, 1984, p. 29.

Occurrence.—Southern Brazil to Tierra del Fuego.

Material examined.—MCZ(M) 3656 (Rio de Janeiro, Brazil), 3659 (Possession Bay, Straits of Magellan), 5690 (Río Negro, Patagonia), 109409 (Mar de la Plata, Argentina), 198433 (San Antonio, Río Negro, Patagonia), 201351 (Punta del Este, Uruguay), 296197 (Salt Pond, Possession Bay, Straits of Magellan), 296204 (Cassino Beach, Patagonia), 296205 (Río Negro, Patagonia), 296206 (Río Negro, Patagonia), 296207 (Praia de Copacobana, Dist. Federal, Argentina), 296208 (Brazil), 296209 (Brazil), 296210 (Río Negro, Patagonia), 296211 (Rio Grande do Sul, Brazil), 296212 (Río Negro, Patagonia); USNM 16819 (Río Negro, Patagonia), 102838 (Rio de Janeiro, Brazil), 131452 (Río Colorado, Argentina), 270866 (Arroyo Miguelete,

[4] often cited as King.

[5] The attribution of this species to Valenciennes by Kiener is apparently either an error, or Valenciennes' original description was never published.

Uruguay), 349195 (Cape Polonia, Uruguay), 362718 (Cabo Santa Maria, Rocha, Uruguay), 365333 (La Paloma, Uruguay), 465591 (Monte Hermosa, Argentina), 780095 (La Paloma, Uruguay), 780097 (Mar de La Plata, Patagonia), 807978 (Saco de Manguerira, Rio Grande do Sul, Brazil), 807979 (Maldonado, Uruguay); ANSP 34621, 34792 (Río Negro, Patagonia), 191485 (Santos, Brazil), 217268 (Solis, Uruguay), 219918 (Maldonado, Uruguay), 236036 (Mar de La Plata, Patagonia), 249072 (Praia do Cassino, Rio Grande do Sul, Brazil), 253100 (La Paloma, Rocha, Uruguay), 312350 (Mar de La Plata, Patagonia) [total: 131 specimens].

Description.—Average to large for subgenus, largest specimens approximately 50 mm total height. Spire relatively high, one-half to one-third total height; body whorl large but not extremely inflated. Protoconch large and paucispiral, consisting of not more than two whorls. Protoconch–teleoconch boundary gradational, distinguished only by initiation of axial ribbing on about the third whorl. Subsutural band appears on about fourth whorl, disappearing with axial ribbing usually by seventh or eighth whorl, corresponding to height of 8–10 mm. Soon after disappearance of axial ribbing, sharp tubercles develop (eventually 14–16 per whorl) on widening subsutural shoulder, increasing in size with succeeding whorls. Profundity on early whorls and rate of increase in size variable. Subsutural band may persist on later whorls, often as multiple, closely-spaced lines between tubercles and suture. Aperture relatively large, with slight posterior notch. Parietal callus usually faint. Ridge at posterior boundary of fasciole may form pronounced carina in large specimens, and anterior boundary may bear one or two tubercles or teeth. Closely spaced, fine, spiral grooves often present around base of body whorl, immediately posterior to fasciole.

Color patterns of brown and white bands, usually consisting of a brown band at the whorl shoulder or subsutural region, and one two-thirds of the way down body whorl, the latter normally being obscured by subsequent whorls. Some specimens coated by a black varnish, partly or wholly obscuring color pattern.

Remarks.—This species is unique among South American species of *Buccinanops* in its conspicuous spinose sculpture, brown- and white-banded color pattern, and for being the only Recent American species to be frequently assigned to the genus *Dorsanum* Gray, 1847. The reason for this assignment would appear to be the presence of axial ribbing on early teleoconch whorls. The very different adult size and form of the protoconchs (and developmental modes) in *moniliferum* and *Dorsanum miran* (Bruguière, 1789), together with their overall shell forms, suggest, however, that these species are not closely related.

Bullia (Buccinanops) uruguayensis Pilsbry
Plate 2, figure 8

Bullia uruguayensis Pilsbry, 1897b, p. 6.
Bullia cochlidium (Dillwyn). Ihering, 1907, p. 445 [*fide* Carcelles and Parodiz, 1939, p. 760] [*non cochlidium* Chemnitz *in* Martini and Chemnitz, 1795, *nec* Dillwyn, 1817, *nec* Kiener, 1834].
Buccinanops uruguayensis (Pilsbry). Carcelles and Parodiz, 1939, pp. 760ff, fig. 12; Carcelles, 1944, pp. 250–251; Barattini and Ureta, 1960, pp. 115–116.
Bullia (Buccinanops) uruguayensis Pilsbry. Cernohorsky, 1982, p. 17-240.
Buccinanops uruguayense (Pilsbry). Cernohorsky, 1984, p. 30.

Occurrence.—Uruguay to northern Argentina.
Types.—ANSP 70507 (eight syntypes).
Type locality.—Maldonado Bay, Uruguay.
Material examined.—MCZ(M) 225883 (La Paloma, Rocha, Uruguay); USNM (?) 183343, (?) 331317 (Maldonado Bay, Uruguay), (?) 331318 (Lobos Island, Uruguay), (?) 807980 (Mar de La Plata, Patagonia); ANSP 70507 (Maldonado Bay, Uruguay [types]), 72648 (Monte Hermosa, Argentina), 253118 (Portezuelo, Maldonado, Uruguay), 312330 (Chapad Malal, Buenos Aires Province, Argentina) [total: 19 specimens].

Description.—Small for subgenus, total height not exceeding 25 mm. Similar to unshouldered individuals of *B. cochlidia* (Dillwyn, 1817) in general form, relative spire height, aperture size and body whorl shape. Protoconch large and paucispiral, consisting of two to three whorls; boundary with teleoconch indistinct. Axial ribs present in early teleoconch whorls, but less prominent than in *cochlidia*. Most individuals show three or four subsutural spiral lirae on fourth or fifth teleoconch whorl persisting to adult whorls. Terminal columellar fold pronounced; columella otherwise simple. Color off-white to gray.

Remarks.—This small form most closely resembles *B. cochlidia* (Dillwyn, 1817) in overall dimensions and general pattern of sculpture, but differs in adult size and details of sculpture.

Bullia (Buccinanops) deforme (King and Broderip)
Plate 2, figure 13

Buccinum deforme King and Broderip, 1831[6], p. 349.
Bullia deformis (King). Reeve, 1846, species 21, pl. 3, fig. 21; Adams and Adams, 1858, p. 113; Kobelt, 1877, p. 290; Tryon, 1882, p. 11, pl. 5, fig. 51; Ihering, 1895, p. 227.
Bullia (Buccinanops) deforme (King). Paetel, 1888, p. 116.
Buccinanops deformis (King). Carcelles and Parodiz, 1939, pp. 762ff, fig. 11; Rios, 1970, p. 92, pl. 27; Rios, 1975, p. 96, pl. 27, fig. 399.
Buccinanops deformis (King). Barattini and Ureta, 1960, p. 116.
Bullia (Buccinanops) deformis (King and Broderip). Cernohorsky, 1982, p. 17-238.
Buccinanops deforme (King and Broderip). Cernohorsky, 1984, p. 27.

[6] often cited as King.

Occurrence.—Patagonia and Uruguay.

Material examined.—MCZ(M) 109427 (Puerto San Antonio, Patagonia), 198435 (Puerto Belgrano, Patagonia), 238325 (Buenos Aires, Argentina), 238820 (Punta del Este, Uruguay); USNM 185350 (Punta Carretas, Uruguay), 219861 (Monte Hermosa, Argentina), 270864, 334528 (Maldonado, Uruguay), 334528, 364197 (Flores Island, near Montevideo, Uruguay), 381691 (Puerto San Antonio, Argentina); ANSP 70505 (wall of fort, Mar de La Plata, Patagonia [subfossil]), 72654 (Bahia Blanca, Argentina), 107443 (Puerto Madryn, Chubut, Argentina), 217263 (Solis, Uruguay), 219917 (Maldonado, Uruguay) [total: 42 specimens].

Description.—Largest individuals very large for subgenus, reaching 60 mm total height. Spire relatively low, body whorl inflated and rounded in profile. Large specimens show some subsutural shouldering, anterior to which a wide depression acts to form posterior slit or sinus on aperture. Smaller individuals with less inflated body whorl and relatively higher spire. Sutures usually enamelled. External sculpture lacking. Terminal columellar fold pronounced. Large specimens show reflexed siphonal channel across fasciole, but anterior boundary of channel formed by flattening and widening of terminal portion of columella, not distinct ridge or carina as in *Dorsanum* s. s. Color usually uniform pale tan or off-white.

Bullia (Buccinanops) duartei (Klappenbach)
Plate 2, figure 11

Buccinanops duartei Klappenbach, 1961, p. 87, figs. 1a, b; Rios, 1970, p. 92, pl. 27; Rios, 1975, p. 96, pl. 27, fig. 400, Cernohorsky, 1984, p. 28.

Occurrence.—Southern Brazil, Uruguay and Patagonia.

Types.—Holotype, MNHN 0769; Paratypes, MNHN 0770.

Type locality.—La Coronilla, Uruguay.

Material examined.—MCZ(M) 203218 (Punta del Este, Uruguay), 225878 (La Coronilla, Uruguay), 275365 (Capo da Canoa, Brazil), 296180 (Río Negro, Argentina); USNM 381150 (Rocha, Uruguay), 654363 (Rio Grande do Sul, Brazil); ANSP 141225 (Cabo Santa Maria, Uruguay), 219919 (Rocha, Uruguay), 244092 (Chui, Rio Grande do Sul, Brazil), 251800 (Punta de la Coronilla, Uruguay), 251802 (Barra, Rio Grande do Sul, Brazil), 253112 (Chuy, Rocha, Uruguay), 276360 (Rio Grande do Sul, Brazil) [total: 104 specimens].

Description.—Largest specimens small for subgenus, not exceeding 30 mm total height, most 20–25 mm. Spire relatively low; body whorl on large specimens usually somewhat inflated anteriorly, giving a "bottom-heavy" appearance. Protoconch unknown. Operculum smooth-margined with marginal nucleus. Parietal callus faint, extending slightly posterior to aperture; thicker posteriorly in larger specimens. Sutures mostly simple, but some show slight enamelling. Terminal columellar fold pronounced. Fasciole simple with single carina running from anterior siphonal notch around to callus. No external sculpture other than growth increments. Apparently no periostracum; shell color brown to purplish, occasionally with indistinct wide dark bands.

Genus **DORSANUM** Gray, 1847

Type Species (by original designation).—*Buccinum politum* Lamarck, 1822 [= *Buccinum miran* Bruguière, 1789].

Diagnosis.—(same as description of type species [see below]).

Remarks.—In the first thorough description of the genus *Dorsanum*, Fischer (1884) considered only living forms, and included only *D. politum* (Lamarck, 1822) in *Dorsanum* s. s. Cossmann (1901b), however, based his description of the genus not only on the Recent type species but also fossil forms from the Tertiary of Europe. These fossils show rows of tubercles and slightly thickened outer lips, and thus contributed these features to Cossman's concept of the genus, one that has greatly influenced subsequent workers, particularly in Europe (see pp. 83–86)

Dorsanum miran (Bruguière)
Plate 1, figures 14–16

Terebra Miran Adanson, 1757, p. 50, pl. 4, fig. 1.
Buccinum miran Bruguière, 1789, p. 268.
Buccinum vittatum var. Gmelin, 1791, p. 3500.
Buccinum politum Lamarck, 1822 [*non* Röding, 1798], p. 269; Kiener, 1834, p. 20, pl. 8, fig. 27; Deshayes, 1844, p. 165.
Bullia polita (Lamarck). Reeve, 1846, pl. 3, species 19; Paetel, 1888, p. 117 [*non* Tryon, 1882, p. 16, pl. 6, fig. 95, listed as synonym of *Bullia belangeri* Kiener, 1834].
Bullia vitrea Reeve, 1846, species 20, pl. 3.
Pseudostrombus politus Adams and Adams, 1858, p. 113, pl. 12, fig. 4.
Bullia (*Dorsanum*) *politum* (Lamarck). Chenu, 1859, p. 160, fig. 753.
Bullia (*Pseudostrombus*) *polita* (Lamarck). Kobelt, 1877, p. 292; Tryon, 1882, p. 15, pl. 6, figs. 88, 89.
Dorsanum politum (Lamarck). Dautzenberg, 1890, p. 165.
Dorsanum miran (Bruguière). Dautzenberg, 1891, p. 23; Dautzenberg, 1910, p. 58; Dollfus, 1911, p. 26, pl. 1, figs. 15, 16; Dautzenberg, 1913, p. 34; Pallary, 1920, p. 37.
Bullia (*Dorsanum*) *miran* (Bruguière). Thiele, 1929, p. 322; Fischer-Piette, 1942, p. 160, pl. 2, figs. 7, 8; Cernohorsky, 1982, p. 17-239.
Bullia miran (Bruguière). Thiele, 1931, p. 322; Nickles, 1947, p. 10; Nickles, 1950, p. 101, fig. 171; Buchanan and Anderson, 1955, p. 58; Knudsen, 1956, p. 46; Marche-Marchad, 1958, p. 28; Pasteur-Humbert, 1962, p. 89; Ansell and Trevallion, 1970, p. 373; Adam and Knudsen, 1984, pp. 69–72, pl. 5, figs. 7, 8, text-fig. 63.
Dorsanum (*Dorsanum*) *miran* (Bruguière). Cernohorsky, 1984, p. 29, fig. 97.

Occurrence.—Senegal, Gabon, Gold Coast, Ivory Coast, South Africa (?).

Material examined.—MCZ(M) 133727 (Gambia), 173329 (Hann, Dakar, Senegal), 201920 (Thiaroye, Dakar, Senegal), 201967 (Joal, Senegal), 296213 (West Africa), 296221 (no locality given); USNM 6809 (Senegal), 13488, 41270 (West Africa), 131459 (Algoa Bay, South Africa ?), 617323 (Dakar, Senegal), 714530 (Senegal); IRSNB P. Dautzenberg collection, I.G. 10.591 (Rufisque Bay, Angola) [total: 26 specimens].

Description.—Larvae initially planktonic. Body bears short cephalic tentacles and well-developed eyes but no posterior metapodial tentacles. Total height of adult shells usually not exceeding 30 mm. Shell usually smooth and polished. Periostracum lacking. External sculpture variable; usually lacking entirely but axial ribs occasionally present on early teleoconch, becoming obsolete on later whorls. Terminal columellar fold pronounced. Anterior notch deep and twisted slightly abaperturally. Deep, distinct reflexed siphonal channel, bordered by strong carinae, extending from notch around fasciole. Parietal callus thin, barely extending out of aperture. Interior of outer apertural lip usually smooth, but occasionally bearing faint denticles. Apex acute; protoconch I smooth and very small, protoconch II may bear axial ribs but more often smooth; protoconch–teleoconch boundary indistinct. Sutures unenamelled. Shell tan to pale brown in color; usually shiny.

INCERTAE SEDIS

Genus **BULLIA** Gray *in* Griffith and Pidgeon, 1834

"**Bullia**" **gruveli** (Dautzenberg)

Dorsanum Gruveli Dautzenberg, 1910, pp. 56–57, pl. 2, fig. 7; Dautzenberg, 1913, p. 33.
Bullia (*Dorsanum*) *gruveli* (Dautzenberg). Cernohorsky, 1982, p. 17-239.
Dorsanum (*Dorsanum*) *gruveli* Dautzenberg. Cernohorsky, 1984, p. 28.
Bullia gruveli (Dautzenberg). Adam and Knudsen, 1984, pp. 68–69, pl. 5, figs. 5, 6, text-figs. 61, 62.

Occurrence.—Bilaouak, Senegal, Mauritania.

Material examined.—None.

Remarks.—Although placed by Cernohorsky (1984) in *Dorsanum* as a close relative of *D. miran* (Bruguière, 1789), this species shows a number of important differences from *Dorsanum* s. s. In overall shell form, it is much higher spired than *D. miran*. Strong axial ribs are present on late as well as early whorls. The siphonal fasciole of *gruveli* does not show the deep, double-sided siphonal channel that distinguishes *D. miran*, nor is there a pronounced terminal columellar fold. Although direct information on reproductive mode does not seem to be available for this species, Adam and Knudsen (1984, p. 69) describe the protoconch of *gruveli* as consisting of approximately one-and-one-half whorls, compared to approximately two-and-one-half whorls in *miran*. The species accepted by Cernohorsky (1984) within *Bullia* s. s. (see Table 2) include a range of shell form and sculpture within which *gruveli* could conceivably fall, although such judgement is hindered by the lack of a thorough study of these species. On the basis of overall morphology and protoconch form then, this species seems to resemble *Bullia* s. s. more closely than it does *Dorsanum* s. s.

"**Bullia**" **terebraeformis** (Dautzenberg)
Plate 1, figures 10, 12

Dorsanum terebraeforme Dautzenberg, 1913, p. 33, pl. 1, figs. 39, 40.
Dorsanum terebreformis [*sic*] Odhner[7]. Peile, 1937, p. 186, fig. 23.
Bullia terebraeformis (Dautzenberg). Nickles, 1947, p. 10; Marche-Marchad, 1958, p. 28.
Bullia (*Dorsanum*) *terebraeformis* Dautzenberg. Cernohorsky, 1982, p. 17-240.
Dorsanum (*Fluviodorsum*) *terebraeformis* Dautzenberg. Cernohorsky, 1984, p. 30, figs. 99, 100.
Bullia terebraeformis (Dautzenberg). Adam and Knudsen, 1984, pp. 73–74, pl. 5, fig. 10, text-figs. 65, 66.

Occurrence.—Angola, Senegal.

Material examined.—IRSNB (two syntypes, P. Dautzenberg collection, I. G. 10.591 (Mossamedes Bay, Angola).

Remarks.—(see below, under "*Bullia*" *granulosa*).

"**Bullia**" **granulosa** (Lamarck)
Plate 1, figures 8, 11

Terebra granulosa Lamarck, 1822, p. 291.
Bullia turrita Gray. Reeve, 1846–1847, species 16, pl. 3 [*fide* Cernohorsky, 1984, p. 30] [*non* Gray, 1839].
Bullia granulosa Tryon, 1882, p. 14, pl. 6, fig. 91; Nickles, 1950, p. 101, fig. 172; Buchanan, 1954, p. 37; Paes-Da Franca, 1955, p. 28; Bernard, 1984, p. 78, pl. 33, fig. 137; Adam and Knudsen, 1984, pp. 66–68, pl. 5, fig. 3, text-figs. 59, 60.
Bullia (*Adinus*?) *crosseana* Tapparone-Canefri, 1882, p. 23, pl. 2, figs. 1,2.
Bullia (*Pseudostrombus*) *fusca* Craven, 1882, p. 16, pl. 2, fig. 1 [*non Bullia fuscus* Gray *in* Dieffenbach, 1843].
Fluviodorsum fusca (Craven). Boettger, 1885, p. 188.
Dorsanum granulosum Dautzenberg, 1913, p. 34.
Nassa semistriata Knudsen, 1956, p. 55 [in part].
Bullia (*Bullia*) *vittata* (Lamarck) [*sic*] [in part]. Cernohorsky, 1982, p. 17-240.
Dorsanum (*Fluviodorsum*) *granulosum* (Lamarck). Cernohorsky, 1984, p. 28, fig. 98.

Occurrence.—West Africa, Gold Coast to Zaire.

Material examined.—MCZ(M) 173330 (Accra, Gold Coast); IRSNB P. Dautzenberg collection, I. G. 10.591 (Zaire River estuary) [total: 13 specimens].

Remarks.—This species and *terebraeformis* Dautzenberg, 1913 were placed in the genus *Dorsanum* Gray,

[7] also spelled *terebriformis*; Peile's citation of Odhner is in error.

1847, subgenus *Fluviodorsum* Boettger, 1885, by Cernohorsky (1984) largely on the basis of similarity in radular form (see Text-fig. 3). Both *terebraeformis* and *granulosa* (Lamarck, 1822) are much more high-spired than *D. miran* (Bruguière, 1789); both bear axial, spiral, and tubercular sculpture, and lack the columellar features characteristic of *D. miran*. They differ, however, in the form of their protoconchs. Adam and Knudsen (1984) report that the protoconch of *granulosa* consists of approximately one-and-three-quarters whorls, while that of *terebraeformis* consists of approximately three whorls; this is confirmed by examination of their specimens (Pl. 1, figs. 10, 12). The correct generic assignment(s) of these two forms is problematical and data on soft parts are badly needed. Based on shell characters alone, however, they appear to be intermediate between the two groups represented by living *Dorsanum* and *Bullia*.

Genus **ADINOPSIS** Odhner, 1923

Type species.—*Adinopsis skoogi* Odhner, 1923.

"Adinopsis" skoogi Odhner
Plate 1, figures 5–7

Adinopsis skoogi Odhner, 1923, p. 15, pl. 1, figs. 11–14; Thiele, 1931, p. 741; Peile, 1937, p. 186, fig. 24; Nickles, 1950, p. 102, fig. 174; Paes-Da Franca, 1955, p. 27; Barnard, 1959, p. 143; Cernohorsky, 1984, p. 27.
Bullia (*Adinopsis*) *skoogi* (Odhner). Cernohorsky, 1982, p. 17-240.
Bullia skoogi (Odhner). Adam and Knudsen, 1984, pp. 72–73, pl. 5, fig. 9, text-fig. 64.

Occurrence.—Angola (Adam and Knudsen, 1984).

Material examined.—ANSP 334519 (Gulf of Guinea, West Africa) [total: three specimens].

Remarks.—*Adinopsis* Odhner, 1923 is a primary homonym of *Adinopsis* Cameron, 1918 in Coleoptera, and is therefore unavailable as a generic name for this species (Cernohorsky, 1984, p. 27).

The protoconch of this species is very large, blunt and paucispiral, consisting of approximately one-and-one-half whorls. A specimen figured by Adam and Knudsen (1984) shows moderately pronounced spiral ridges uniformly covering the entire outer surface of the shell. Specimens in the ANSP collection, however, show much less conspicuous, fine spiral grooves over the whole surface. At least some specimens show striations or faint denticles on the interior of the outer lip. The shell is relatively thin and lacks a well-developed parietal callus in smaller specimens. Larger specimens may show a thin plate of callus offset from the columella by a slit, in this somewhat resembling some species of *Nassarius*. There is a terminal columellar fold, although this too varies in its expression with the size of the shell. In general, the terminal columellar fold is less pronounced than in *Dorsanum miran* (Bruguière, 1789), but more than in most species of *Bullia* s. s. The ANSP specimens are labeled as having been dredged from a depth of 90 m, which if accurate would probably make this the deepest record for a member of the *Bullia* group.

Cernohorsky (1984) has suggested that "*A.*" *skoogi* belongs in Nassariinae rather than the *Bullia* group. As discussed in the phylogenetic analysis on p. 107, this species appears to be more closely allied to members of the *Bullia* group than to nassariines; within the *Bullia* group it seems to be intermediate between the two principal branches.

Genus **ADINUS** Adams and Adams, 1853

Type species.—*Bullia truncata* Reeve, 1846.

Adinus truncatus (Reeve)
Plate 1, figure 4

Bullia truncata Reeve, 1846, species 15, pl. 3.
Pseudostrombus (*Adinus*) *truncatus* (Reeve). Adams and Adams, 1858, p. 114.
Adinus truncatus (Reeve). Cernohorsky, 1984, pp. 23, 26, fig. 101.

Occurrence.—Unknown.

Type.—BM(NH) [figured by Cernohorsky, 1984, fig. 101].

Material examined.—ANSP 34615 (no locality given).

Remarks.—This species departs even further from the typical shell form of the *Bullia* group, and in fact all nassariids, than do the preceeding problematic species. It is very high-spired, with a very small body whorl and aperture. The columella is truncated, but does show a slight terminal fold. The outer apertural lip is denticulate and thickened. Cernohorsky (1984, p. 26) reports that the protoconch is paucispiral, and that the shell surface is "sculptured with minutely punctate spiral grooves." The locality of the type specimen is apparently unknown; four fossil species from the Tertiary of Indonesia have been allied with the genus (Cernohorsky, 1984, p. 26).

Cernohorsky suggests that this species is a buccinid. Given the currently poor definition of Buccinidae, however, such an assignment by itself is relatively uninformative. Its very high spire and truncated columella probably exclude *Adinus truncatus* from Nassariidae (and certainly from the *Bullia* group), but its exact taxonomic position remains undetermined.

FOSSIL REPRESENTATIVES

MIOCENE OF THE MIDDLE ATLANTIC COASTAL PLAIN

Introduction

Representatives of *Bulliopsis* Conrad, 1862a are usu-

ally rare and inconspicuous components of the well-preserved Miocene molluscan faunas of Maryland, Virginia, and New Jersey. For more than a century authors have speculated on the relationship of these forms to living *Bullia* s. s., but these suggestions have never been evaluated critically. More recent summaries (*e.g.*, Vokes, 1957) have recognized three species of *Bulliopsis* Conrad, 1862a from Maryland and Virginia. The relationships of these taxa to each other, and to a fourth species from New Jersey, have not been studied in detail.

Examination of a large sample of Maryland and Virginia specimens suggests that evolution within this small group was more complex than previously recognized, and allows assessment of their phylogenetic position relative to the New Jersey form, as well as to similar Eocene specimens and to the *Bullia* group as a whole. Morphological evolution within Miocene *Bulliopsis* from Maryland and Virginia appears to have occurred both anagenetically and cladogenetically (Allmon, 1985). The group is closely related to, but evolved separately from, the lineage leading to living species of *Buccinanops* d'Orbigny, 1841. Miocene species of *Bulliopsis* were among the last surviving members of the *Bullia* group in the northern hemisphere, dwindling to extinction in the uppermost Miocene.

Previous Work

Bulliopsis was first described by Conrad (1830, p. 226) from Miocene beds exposed along the St. Mary's River, St. Mary's Co., Maryland, as *Nassa quadrata*:

> Shell turreted; spire with the whorls rather square, and slightly projecting at the angles; left lip reflected over the columella, and thickened above.

Conrad also observed that there was some degree of heterogeneity in this new species, adding that some specimens showed "traces of tubercles on the angles of the whorls."

In 1842, Conrad assigned *N. quadrata* to the genus *Buccinum* Linnaeus, 1758. He also described another species, *B. integrum*, as follows:

> shell short, subfusiform or elliptical, smooth; destitute of ribs or striae; spire conical, the volutions convex; . . . columella thick; labium reflected. (Conrad, 1842, p. 194)

Twenty years later, Conrad (1862a) listed three species of the genus *Bullia*, subgenus *(Bulliopsis)* Conrad as follows:

> (1) *B. ovata*—Smooth; last whorl subquadrate; ovate or oblong-ovate, entire; whorls 5 or 6, slightly convex; spire conical, about half the length of the shell; aperture eliptical.
>
> Locality. St. Mary's Co., Maryland.
>
> Shorter and broader than the other two species of Maryland, the callus not prominent nor extending beyond the upper extremity of aperture.
>
> (2) *B. marylandica*—Oblong ovate, entire; whorls 6, slightly convex or subtruncated laterally; suture impressed, aperture about half the length of the shell; columella profoundly callous above, the callus extending beyond the lip.
>
> Locality. St. Mary's Co., Maryland.
>
> Proportionally larger than the proceding, and the spire subscalariform. The shell is variable in outline, the spirebeing much longer in some specimens than others of equal breadth.
>
> (3) *B. quadrata*. Conrad.

Conrad added that "There are no known living representatives of this subgenus."

In a separate paper later in the same volume, however, Conrad revised this arrangement, including these species in the genus *Tritia* Adams, 1852 (*ex* Risso MS), but retained them in the subgenus *Bulliopsis* (Conrad, 1862b, pp. 562–563).

In 1866, Conrad (1866b, pp. 65–66) once again altered his classification, still retaining the subgenus but placing *marylandica*, *integra*, *quadrata*, *integra* var. *ovata*, and the new species *subcylindrica* back into the genus *Nassa* Lamarck, 1799. Finally, in 1868, Conrad referred *marylandica*, *quadrata*, and *integra* to the genus *Melanopsis* Ferussac, 1807[8].

Fischer (1887, p. 703) supported the synonymy of *Bulliopsis* with *Melanopsis*. Harris (1899a, p. 58), however, disagreed, stating that he was "not sure but *Bulliopsis* should be put under *Buccinanops*, *i.e.*, *Bullia*." Martin (1904) summarized all work on the group up to that time. He raised *Bulliopsis* to generic rank within the family Nassidae, and recognized three species: *B. integra*, *B. quadrata*, and *B. marylandica*.

Vokes (1957, p. 32) gave the following brief summary:

> Representatives of the genus *Bulliopsis* are moderately common in and wholly distinctive of the St. Mary's Formation. Three species have been described: *Bulliopsis quadrata* (Conrad); *B. marylandica* (Conrad); and *B. integra* (Conrad). The differences between the first two are clear from [Martin's (1904)] illustrations.
>
> *B. integra* most closely resembles *B. marylandica* in lacking the shoulder on the whorl but differs in having a shorter more inflated body whorl and a proportionately higher spire, and the callus on the inner lip is not as thickly developed.

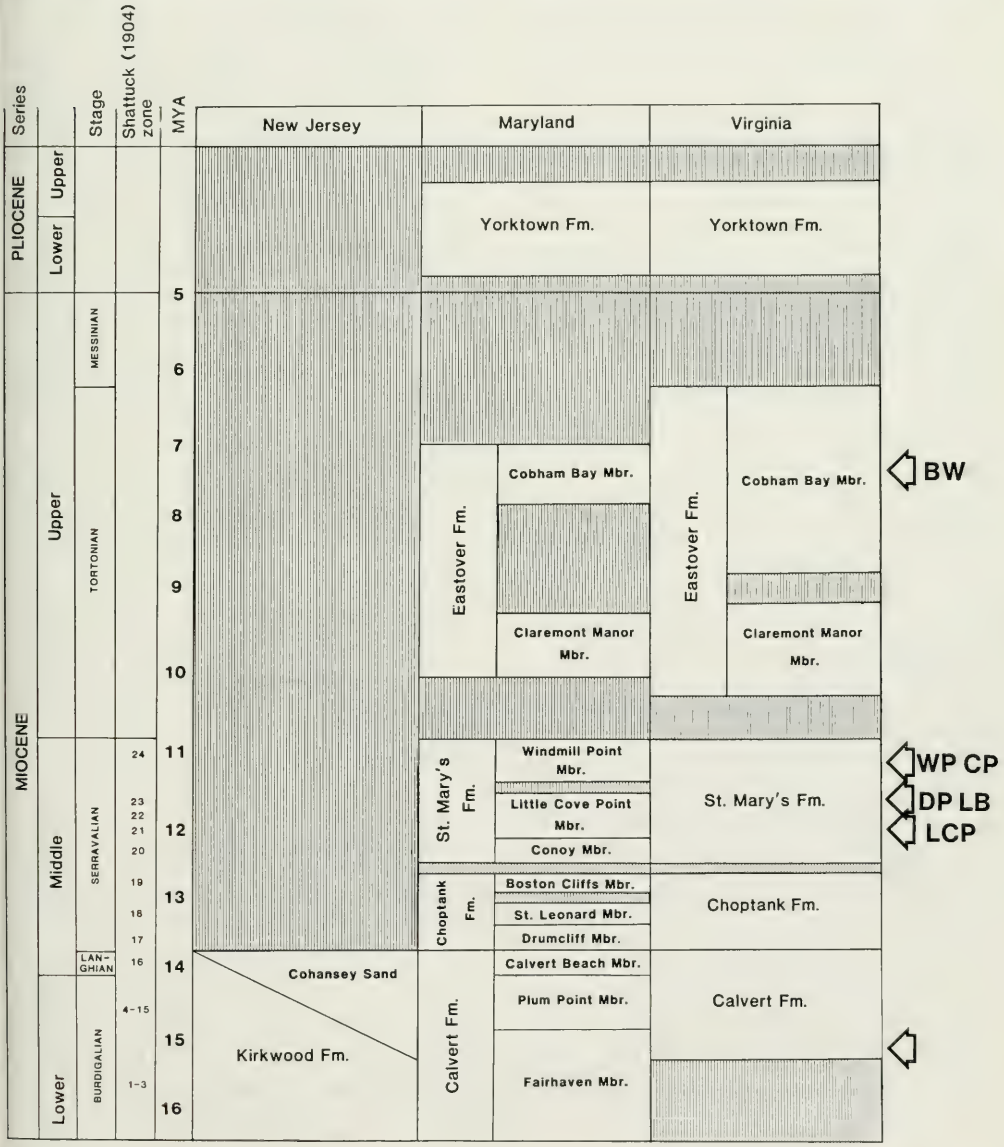
[8] It is possible that these frequent taxonomic changes did not reflect real changes in Conrad's opinion of the relationships of these forms. Conrad was apparently almost pathologically forgetful (Wheeler, 1935; Moore, 1962), and may actually not have remembered whether or what he had previously named these species.

Text-figure 5.—Generalized stratigraphic classification for Miocene and early Pliocene sediments of the Middle Atlantic coastal plain. Vertically-ruled areas indicate hiatuses (based on Ward, 1980, 1985, [in press]; Blackwelder and Ward, 1976). Arrows on right show approximate stratigraphic position of collecting localities: **BW** = Bowler's Wharf, loc. 6; **WP** = Windmill Point, loc. 3; **CP** = Chancellor Point, loc. 4; **DP** = Deep Point, loc. 5; **LB** = Langley's Bluff, loc. 2; **LCP** = Little Cove Point, loc. 1. Lower unlabeled arrow indicates approximate stratigraphic position of occurrence of *Bulliopsis* in the Kirkwood Formation at Cape May, New Jersey.

Present Study

Stratigraphic Context

On the Atlantic coastal plain, *Bulliopsis* is found in sediments of the Chesapeake Group, a series of fine to coarse sands, silts, and clays deposited under shallow marine conditions between approximately four and 20 million years ago (ma) (middle early Miocene–early Pliocene). In Maryland and Virginia, the Chesapeake Group includes, in ascending order, the Calvert, Choptank, St. Mary's, Eastover, and Yorktown Formations. In New Jersey, the Kirkwood Formation appears to be



equivalent to the lower portion of this sequence (see p. 50). Species of *Bulliopsis* are known to occur throughout the St. Mary's in Maryland, in the upper Eastover in Virginia, and in the subsurface Kirkwood in New Jersey. The stratigraphic framework employed here is based on recent revisions of the upper portion of the Chesapeake Group (Blackwelder and Ward, 1976; Ward and Blackwelder, 1980; Ward, 1980; Ward, 1985; Ward, *in press*), summarized in Text-figure 5.

St. Mary's Formation.—This name was first used by Shattuck (1902, 1904) to refer to beds exposed along the Calvert Cliffs in Calvert County, Maryland, and along the St. Mary's River in St. Mary's County, Maryland. Blackwelder and Ward (1976) suggested that the Conoy Member of the Choptank Formation be placed in the St. Mary's Formation. The Conoy is a poorly fossiliferous, silty clay unconformably overlying the Boston Cliffs Member of the Choptank Formation. *Bulliopsis* is not known from this unit. Blackwelder and Ward (1976) also suggested the informal name "Little Cove Point unit" for a series of lithologically similar, sparsely fossiliferous clays and richly fossiliferous clayey sands unconformably overlying the beds of the Conoy Member. Ward [*in press*] designates this unit the Little Cove Point Member of the St. Mary's Formation. The Little Cove Point unit is named for its best exposure at Little Cove Point on the western shore of the Chesapeake Bay, Calvert County, Maryland (loc. 1, p. 32). The sandy layers at this locality contain *Bulliopsis*. The section at Little Cove Point has been described in detail by McCartan, Blackwelder, and Lemon (1985).

Ward (1980) informally designated as the "Deep Point beds" a series of medium to coarse clayey sands conformably overlying the Little Cove Point beds, but subsequently (Ward, 1985; Ward, *in press*) has included them in the Little Cove Point unit. The Deep Point beds are exposed at Deep Point on the St. Mary's River, St. Mary's County, Maryland (loc. 5, p. 34), and at Langley's Bluff on the western shore of the Chesapeake Bay, St. Mary's County, Maryland (loc. 2, p. 33). *Bulliopsis* is present in these beds at both localities.

Blackwelder and Ward (1976) used the informal name "Windmill Point beds" for a medium-grained, well-sorted shelly sand unconformably overlying the rest of the St. Mary's Formation, and separated from it by a hiatus of perhaps 100,000–300,000 years (Ward, oral commun., 1985). Ward [*in press*] designates this unit as the Windmill Point Member of the St. Mary's. Beds of the Windmill Point Member exposed at Windmill Point and Chancellor's Point on the St. Mary's River, St. Mary's County, Maryland (locs. 3, 4, pp. 33, 34), are very fossiliferous and contain *Bulliopsis*. The Windmill Point Member extends south into Virginia and remains highly fossiliferous. It is represented by a deeper-water facies here, however, (Ward, oral commun., 1987; Ward, *in press*) and at localities such as Essex Mill, Essex County (USGS loc. 26091; loc. 9 in Text-fig. 6), *Bulliopsis* is not present.

Eastover Formation.—This formation was defined by Ward and Blackwelder (1980) to include beds underlying the Yorktown Formation and overlying the St. Mary's Formation. The Eastover consists of a lower bed, the Claremont Manor Member, and an upper bed, the Cobham Bay Member. The Claremont Manor consists of poorly sorted, coarse to fine, silty and clayey sands grading into clays. It is poorly fossiliferous, and apparently contains no *Bulliopsis*.

The Cobham Bay Member unconformably overlies the Claremont Manor, and consists across most of its geographic extent of a fine-grained shelly sand. Locally, however, structural features appear to have caused semi-isolation of small basins, and clays have accumulated (Ward and Blackwelder, 1980). Bowler's Wharf, on the Rappahannock River in Virginia (loc. 6, p. 34), is such an area. Molluscan diversity and abundance are much lower in these clay beds than in the surrounding sandier facies, which contain a diverse assemblage. *Bulliopsis* does not occur in most beds of the Cobham Bay. It is relatively common, however, in the clayey facies in the region around Bowler's Wharf. It is present, but rare, in apparently isolated horizons of the sandy facies, such as are exposed at Union Mill, Essex County. The Eastover Formation is separated from the overlying Yorktown Formation by a major hiatus, above which *Bulliopsis* is not known to occur.

Throughout the Miocene, basins of deposition shifted gradually southward along the Atlantic coast (Ward, 1985; Ward and Strickland, 1985). This is illustrated in Text-figure 7 for the two members of the St. Mary's Formation and the Cobham Bay Member of the Eastover Formation, in which *Bulliopsis* is known to occur.

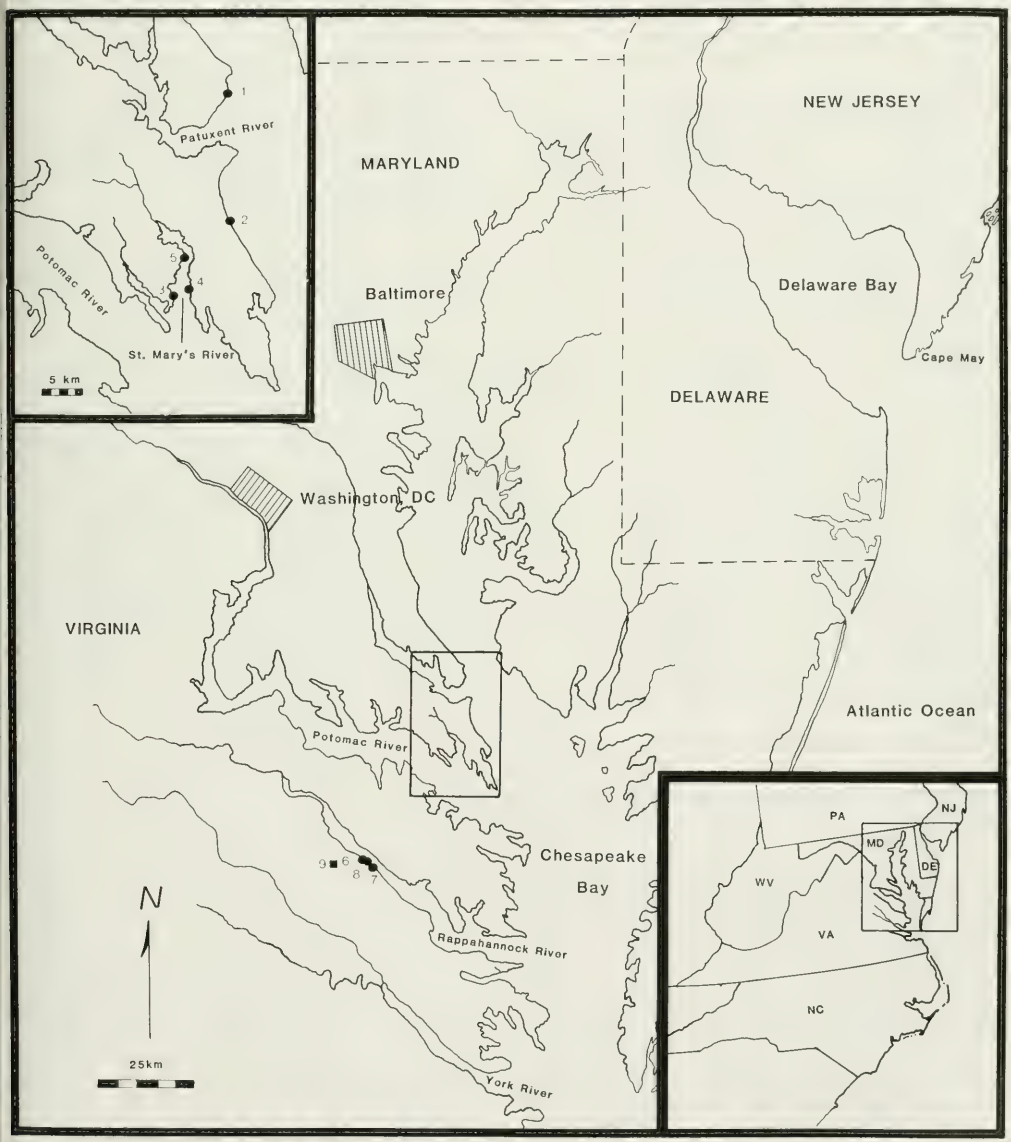
Methods

A total of 431 specimens of *Bulliopsis* collected from six localities in Maryland and Virginia were included in the study. Localities are indicated in Text-figure 6, and described below. Their stratigraphic positions relative to each other are indicated in Text-figure 5.

(1) Little Cove Point (LCP): approximately 3.1 km south of Cove Point Light House, western shore of Chesapeake Bay, Calvert County, Maryland (Solomons Island 7½′ quad.). High cliffs. "Little Cove Point beds", St. Mary's Formation. USGS loc. 25302, loc. 15 of Ward (1980).

(2) Langleys Bluff (LB): 3.2 km southeast of Hermanville, St. Mary's County, Maryland, western shore of Chesapeake Bay. (St. Mary's City 7½′ quad.). Low cliffs. "Deep Point beds", St. Mary's Formation. USGS loc. 25303, loc. 22 of Ward (1980).

(3) Windmill Point (WP): west bank of St. Mary's River, opposite mouth of St. Inigoes Creek, St. Mary's County, Maryland (St. Mary's City 7½′ quad.). Low cliffs. "Windmill Point beds", St. Mary's Formation. USGS loc. 25304, loc. 12 of Ward (1980).



Text-figure 6.—Map of the Chesapeake Bay region showing the localities from which specimens of *Bulliopsis* were collected for the present study, and the location of Cape May, New Jersey.

(4) Chancellor Point (CP): east bank of St. Mary's River, approximately 2.1 km south of St. Mary's City, St. Mary's County, Maryland (St. Mary's City 7½′ quad.). Low cliffs. "Windmill Point beds", St. Mary's Formation. loc. 13 of Ward (1980).

(5) Deep Point (DP): east bank of St. Mary's River, approximately 0.5 km north of Portobello Point, St. Mary's County, Maryland (St. Mary's City 7½′ quad.). Moderately high cliff. "Deep Point beds", St. Mary's Formation. loc. 19 of Ward (1980).

(6) Bowler's Wharf (BW): east bank of Rappahannock River, Essex County, Virginia (Morattico and Dunnsville 7½′ quads.). High to low cliffs 1–2 km downriver. Cobham Bay Member, Eastover Formation. USGS loc. 26026, loc. 2 of Ward (1980) and Ward and Blackwelder (1980).

Table 4 shows the approximate amount of time spent, and the number of *Bulliopsis* specimens collected, at each of these six localities in the course of the present study. Although hours at all localities obviously cannot be regarded as equivalent in every case, these figures may suggest in a general way the differing relative abundances of these gastropods over the time and space covered in this study.

In addition to material collected in the field, approximately 200 specimens of *Bulliopsis* in the USGS, USNM and CMM collections were also examined. Two additional localities were represented in these collections: Layton's Landing (USGS loc. 26027), on the Rappahannock River, Essex County, Virginia, and Union Mill, an outcrop just north of a church at the intersection of Routes 608 and 647, just north of Downing, Richmond County, Virginia (unnumbered USGS loc. of L. W. Ward). These two localities are indicated on Text-figure 6 as localities 7 and 8, respectively.

Two of the three species recognized and figured by Martin (1904; Pl. 7, figs. 1, 2), *B. integra* and *B. marylandica*, are easily distinguished among the available specimens from the Maryland St. Mary's. The specimen labeled by Martin as *B. quadrata* is also representative of a morphotype recognizable in these beds. This is a fairly smooth, straight-sided form with a moderately elevated spire, smaller than *B. marylandica* but less inflated and more elongate than *B. integra*. This specimen agrees more closely, however, with the probable type specimens of *B. subcylindrica* (Conrad, 1866b) than with the probable types of *B. quadrata* (Conrad, 1830) (Pl. 7, figs. 3–10), which show pronounced subsutural shoulders and relatively high spires. Specimens agreeing with *quadrata sensu* Conrad are found only in small numbers in the Maryland St. Mary's. They are much more common in beds of the Cobham Bay Member of the Eastover Formation exposed along the Rappahannock River in Essex County, Virginia. Some specimens agreeing somewhat with *B. subcylindrica* are also present in these beds.

Table 4.—Time analysis for collections of *Bullia* (*Bulliopsis*) recovered from the Miocene of Maryland and Virginia in this study. **LCP** = Little Cove Point (loc. 1); **DP** = Deep Point (loc. 5); **LB** = Langley's Bluff (loc. 2); **WP** = Windmill Point (loc. 3); **CP** = Chancellor Point (loc. 4); **BW** = Bowler's Wharf (loc. 6).

locality	***LCP***	***DP***	***LB***	***WP***	***CP***	***BW***
number of hours (1981–1983)	64	3	13	32	16	16
number of specimens	164	14	8	82	7	23
specimens/hour	2.6	4.7	0.6	2.6	0.4	1.4
number of specimens (1974–1980)	132					

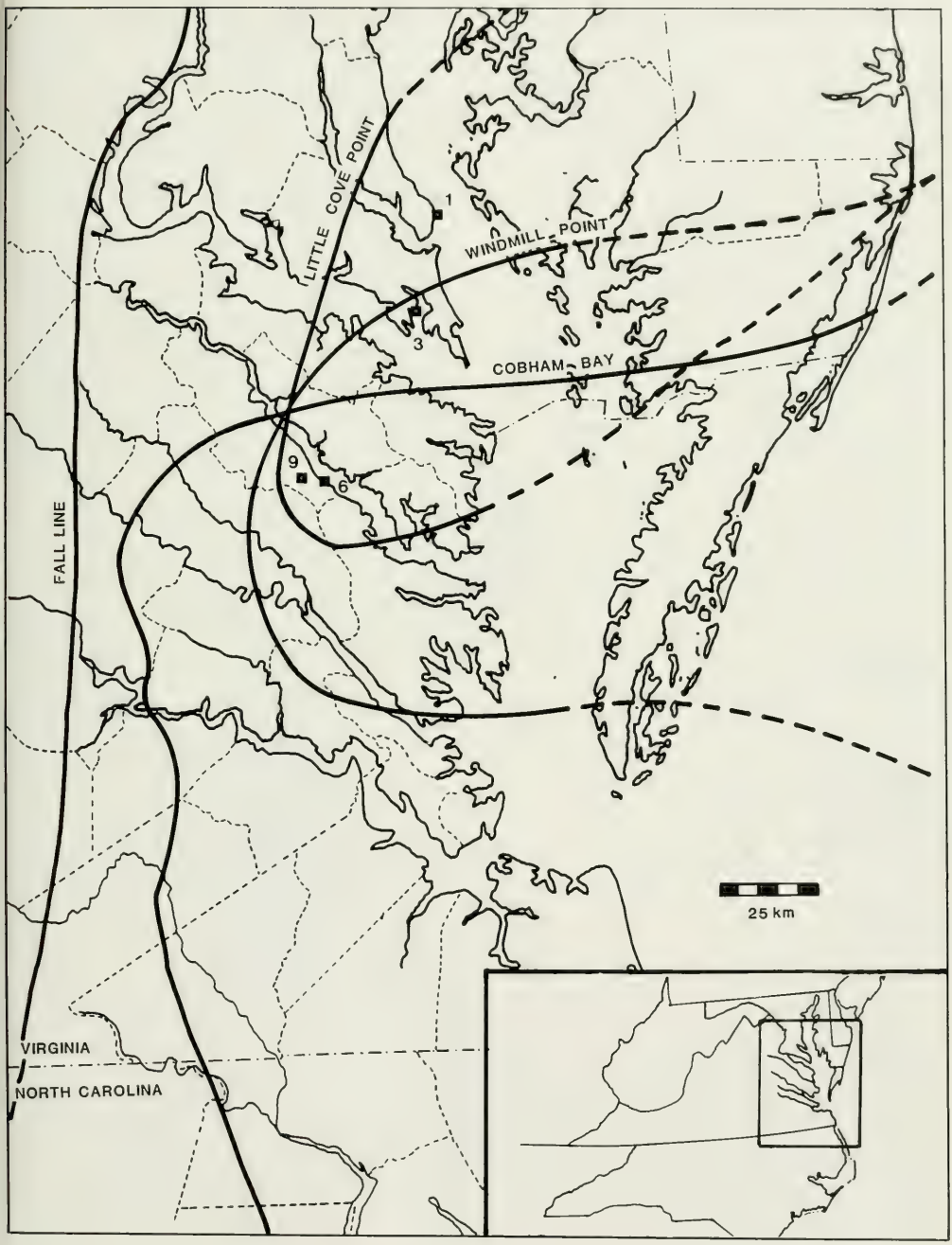
Total number of specimens collected, 430; specimens measured and/or examined in museum collections: USNM, 141; USGS, 50; CMM, 10; total number of specimens in study, 631.

Two systematic hypotheses can be proposed to account for this distribution of morphologies (Text-fig. 8), one recognizing three species-level taxa and one recognizing four. To test these two hypotheses, each of the available Maryland and Virginia *Bulliopsis* specimens was assigned to one of four groups (hereafter referred to as the "total groups"): (1) those agreeing with the syntypes of *B. integra* [ANSP 15688]; (2) those agreeing with Martin's (1904) figured specimen of *B. marylandica* [USNM 353125; ANSP types apparently lost]; (3) all remaining specimens from the St. Mary's Formation in Maryland, most agreeing with the probable types of *B. subcylindrica* [ANSP 15687], but also some with the probable types of *B. quadrata* [ANSP 15686]; and (4) all specimens from the Eastover Formation in Virginia, most agreeing with the types of *B. quadrata*.

To evaluate the range of morphological variation around these distinguishable forms, four groups of specimens that agreed especially well with the types of

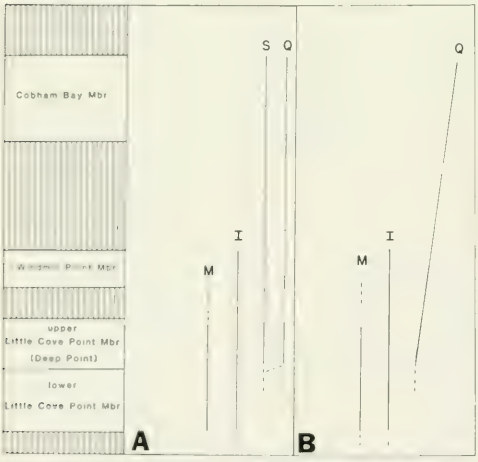
Text-figure 7.—Map of the Middle Atlantic coastal plain of the United States, showing the approximate extent of transgression, and therefore the basin of deposition, during the three major time intervals represented by specimens of *Bulliopsis* from the Miocene of Maryland and Virginia (modified from Ward and Strickland, 1985.)

The basin of deposition for the Little Cove Point Member of the St. Mary's Formation is the oldest, and most northerly of the three. Structural changes caused the basin to shift southward during the time of deposition of the overlying Windmill Point Member. This southward shift continued during the deposition of the Claremont Manor Member of the overlying Eastover Formation (not shown), and latest Miocene Cobham Bay Member, which continued as far south as North Carolina. Major localities for *Bulliopsis* are indicated, corresponding to the localities shown in Text-figure 6 and described in the text. In each of the three intervals, *Bulliopsis* is known only from the more northerly half of the basin (*i.e.*, loc. 1 during deposition of the Little Cove Point, loc. 3 during deposition of the Windmill Point, and loc. 6 during deposition of the Cobham Bay). "Windmill Point beds" are exposed at locality 9 (Essex Mill), but *Bulliopsis* apparently does not occur there.


LITTLE COVE POINT
WINDMILL POINT
COBHAM BAY
FALL LINE
1
3
9
6
25 km
VIRGINIA
NORTH CAROLINA

the four species were chosen, a total of 35 specimens (see Text-fig. 14). These are hereafter referred to as the "select groups". The *B. marylandica* select group consisted of 12 specimens (Text-fig. 14a) from Little Cove Point (Loc. 1); the *integra* select group consisted of nine specimens (Text-fig. 14b) from Little Cove Point, and Deep Point and Windmill Point (Locs. 3, 4); the *subcylindrica* select group consisted of seven specimens (Text-fig. 14c) taken only from total group 3, collected from "Deep Point" and "Windmill Point beds" (Locs. 2, 3, 4, 5); the *quadrata* select group consisted of seven specimens (Text-fig. 14d) taken only from total group 4, collected from Eastover beds at Bowler's Wharf (Loc. 6).

Preservation permitting, 16 variables were measured or calculated on each specimen (Text-fig. 9). A specimen was included in the analysis if values for five or more variables could be obtained; a total of 318 satisfied this requirement. All linear measurements were made directly on the shells with stainless steel dial calipers. The two angular measures were made directly on the shells by means of a rotating straightedge fastened to a protractor. The two shouldering indices (**SH1**, **SH2**) were determined by X-raying the shells, tracing silhouettes from the X-rays, and measuring the lengths and perimeters with an electronic digitizing table connected to a microcomputer (Text-fig. 9). Because of poor condition of the spires of many specimens, only 220 specimens were measured in this way. Mean values and standard deviations for all variables are shown in Table 5.



Text-figure 8.—Alternative scenarios for the evolution of Miocene species of *Bulliopsis*. **A**, *Bulliopsis subquadrata* [**S**] and *Bulliopsis quadrata* [**Q**] are separate species differing in degree of sculpturing, and both persist into the Cobham Bay Member of the Eastover Formation. **B**, All post-St. Mary's *Bulliopsis* belong to a single, variable species, *Bulliopsis quadrata*, [**Q**], which originated in lower or middle St. Mary's time and became increasingly sculptured. **M** = *Bulliopsis marylandica*; **I** = *Bulliopsis integra*. Dashed lines indicate undetermined points of origin and/or extinction.

Text-figure 9.—Morphometric variables recorded for specimens of *Bulliopsis*.

A. Linear and angular measurements made directly on shells of *Bulliopsis*. (1) *shell height* (**SHL**), measured from apex to anteriormost point of inner lip (±0.003 cm); (2) *total shell height* (**TSL**), measured from apex to anteriormost point of the shell, inner or outer lip (±0.003 cm); (3) *body whorl width* (**BWW**), maximum lateral diameter of the body whorl, measured on the ventral side between the posteriormost point of callus and suture between body whorl and spire (±0.003 cm); (4) *total shell width* (**TSW**), maximum lateral diameter measured from labral wall of aperture to opposite side of body whorl (±0.003 cm); (5) *shell thickness* (**STH**), maximum diameter of body whorl measured dorsoventrally (±0.003); (6) *ventral spire height* (**VSH**), measured along midline of shell on ventral side, from apex to suture of the body whorl and spire (±0.05 cm); (7) *dorsal spire height* (**DSH**), measured along midline of shell on dorsal side, from apex to suture of body whorl and spire (±0.05 cm); (8) *aperture length* (**APL**), measured from posteriormost point of aperture opening to anteriormost point of outer lip (±0.05 cm); (9) *callus length* (**CAL**), measured on ventral surface, from posteriormost point of callus on body whorl to anteriormost point of inner lip (±0.05 cm); (10) *aperture width* (**APW**), maximum distance laterally across aperture between inner and outer lips (±0.003 cm); (11) *anterior* (siphonal) *canal width* (**ACW**), lateral distance between anteriormost points of inner and outer lips (±0.05 cm); (12) *height of first spire whorl* (**SWH**), measured along midline of shell on ventral side, from suture between body whorl and spire and suture separating first and second spire whorls (±0.05 cm); (13) *apical angle* (**AAN**), angle subtended by lines on opposite sides of the spire tangent to the whorls of the spire (±5°); (14) *pleural angle* (**PAN**), angle subtended by lines on opposite sides of the spire tangent to the first (abapical) spire whorl and the body whorl (±5°); (15) *shouldering index 1* (**SH1**), ratio of perimeter of spire silhouette, measured (looking ventrally) on left side from body whorl suture to apex, to straightline distance between these points [see Text-fig. 9**B**]; (16) *shouldering index 2* (**SH2**), ratio of partial perimeter of body whorl silhouette, measured (looking ventrally) on the left side from midpoint of shell length to body whorl suture, to the straightline distance between these points [see Text-fig. 9**B**].

From these measured data, four additional shell parameters were calculated for each specimen: (17) *average spire height* (**ASH**) = (**VSH** + **DSH**) ÷ 2; (18) *body whorl length* (**BWL**) = **TSL** − **ASH**; (19) *spire ratio* (**SPR**) = **ASH** ÷ **TSL**; (20) *whorl ratio* (**WHR**) = **SWH** ÷ **TSL**.

B. Shell of *Bulliopsis*, traced from an X-ray, illustrating the method of determining shouldering indices. Point P1 is the shell apex; point P2 is the suture line between the spire and body whorl on the left side of the shell looking ventrally; point P4 is the anteriormost point of the unbroken shell; point P5 is the point halfway between points P1 and P4; point P3 is the point of intersection of a line from point P5 normal to the axial line P1–P4 with the body whorl wall. *Shouldering index 1* (**SH1**) is equal to the curved perimeter distance between points P1 and P2, divided by the straight-line distance between them. *Shouldering index 2* (**SH2**) is equal to the curved perimeter distance between P2 and P3, divided by the straight-line distance between them. All five points were recorded as cartesian coordinates using an electronic digitizer, and lengths were calculated by computer.

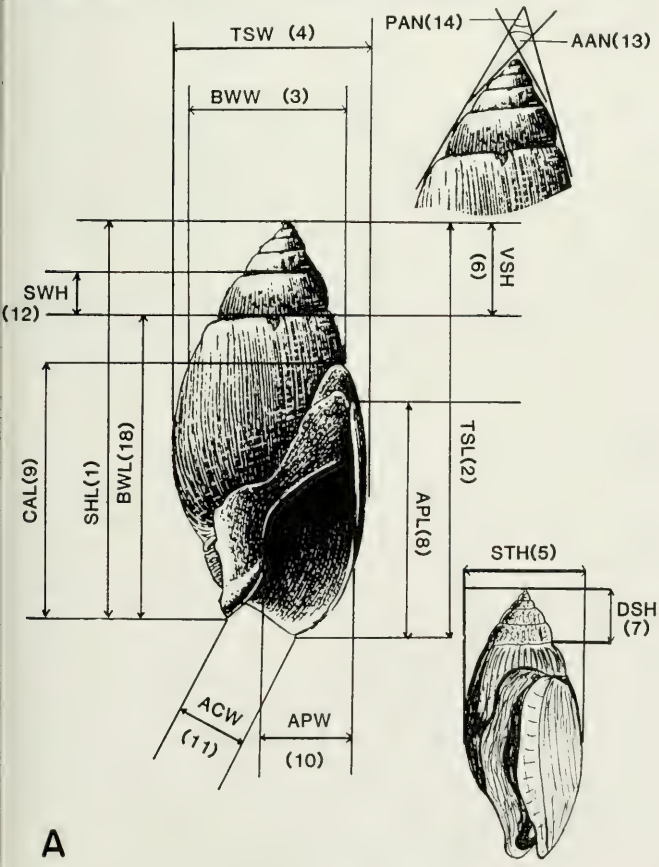
Two types of multivariate analyses were performed on the data matrix using the SPSS-X programming package (SPSS, Inc., 1983).

(1) A Q-mode varimax-rotated factor analysis was performed using the procedure **FACTOR** on the entire matrix. Missing values were replaced by SPSS-X by their means calculated from all other cases in the total matrix. Three factors were reported, explaining a cumulative total of 58.4% of the total variance in the original matrix (Table 6).

(2) The SPSS-X procedure **DISCRIMINANT** was used to perform a discriminant analysis by the Direct Method. In this technique, all variables are entered into the analysis simultaneously, and the discriminant functions are derived directly from the entire set, regardless of the discriminating power of each variable. The groups specified *a priori* were the four select groups described above. Missing values within these groups were replaced with means calculated only from the other specimens in each group. Discriminant scores for the remaining specimens were then reported by the procedure in relation to these designated groups. Missing values in these nonselected specimens were replaced by SPSS-X with mean values calculated from the entire data matrix.

Results

Factor Analysis.—Text-figure 10 shows a plot of scores on the first two factors for all 318 specimens in the analysis. The four select groups are indicated by outlines. The *marylandica–integra* and *subcylindrica–quadrata* select groups form two largely nonoverlapping clusters, and this separation is clearer along the second factor axis than along the first. There is a high degree of overlap of the four total groups with each other.



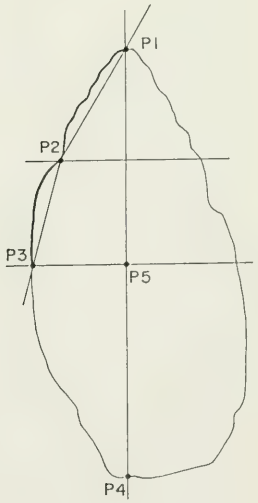


Table 5.—Means and standard deviations (in parentheses) for all measured variables on 334 specimens of *Bullia* (*Bulliopsis*) from Maryland and Virginia. See Text-figure 9 for key to abbreviations of variables.

	marylandica	*integra*	*quadrata (total group 3)*	*quadrata (total groups 3 and 4)*	*quadrata (total group 4)*	*all specimens*
SHL	2.356 (0.386)	1.742 (0.400)	1.763 (0.295)	1.945 (0.404)	2.161 (0.416)	2.194 (0.463)
TSL	2.413 (0.385)	1.429 (0.390)	1.752 (0.336)	1.853 (0.440)	1.982 (0.535)	2.155 (0.555)
BWW	0.940 (0.125)	0.862 (0.207)	0.762 (0.108)	0.847 (0.149)	0.928 (0.138)	0.907 (0.156)
TSW	1.173 (0.190)	0.963 (0.248)	0.859 (0.147)	0.953 (0.196)	1.053 (0.196)	1.103 (0.228)
STH	1.049 (0.174)	0.900 (0.201)	0.793 (0.114)	0.890 (0.176)	0.977 (0.177)	0.992 (0.195)
VSH	0.526 (0.171)	0.398 (0.137)	0.532 (0.117)	0.580 (0.138)	0.633 (0.142)	0.515 (0.169)
DSH	0.725 (0.161)	0.577 (0.190)	0.740 (0.149)	0.796 (0.190)	0.853 (0.214)	0.713 (0.182)
APL	1.198 (0.264)	0.756 (0.167)	0.868 (0.118)	0.968 (0.205)	1.054 (0.227)	0.1069 (0.295)
CAL	1.414 (0.361)	0.783 (0.198)	0.888 (0.175)	0.989 (0.223)	1.095 (0.223)	1.213 (0.411)
APW	0.527 (0.155)	0.323 (0.093)	0.374 (0.056)	0.384 (0.103)	0.395 (0.144)	0.474 (0.163)
ACW	0.331 (0.077)	0.183 (0.044)	0.215 (0.069)	0.207 (0.070)	0.201 (0.073)	0.285 (0.097)
SWH	0.287 (0.098)	0.273 (0.052)	0.286 (0.039)	0.304 (0.066)	0.320 (0.081)	0.288 (0.082)
PAN	75.6 (9.4)	80.8 (13.4)	67.2 (8.1)	67.6 (8.4)	68.4 (9.9)	75.4 (10.5)
AAN	54.2 (7.0)	58.2 (9.9)	46.3 (6.2)	45.4 (7.3)	43.1 (9.5)	54.0 (8.5)
SH1	1.062 (0.018)	1.065 (0.013)	1.070 (0.025)	1.084 (0.035)	1.096 (0.039)	1.067 (0.024)
SH2	1.040 (0.023)	1.022 (0.013)	1.055 (0.026)	1.074 (0.043)	1.098 (0.047)	1.045 (0.032)
ASH	0.620 (0.148)	0.489 (0.160)	0.620 (0.136)	0.691 (0.160)	0.795 (0.141)	
BWL	1.770 (0.336)	0.965 (0.250)	1.080 (0.270)	1.202 (0.316)	1.450 (.256)	
SPR	0.26 (0.05)	0.30 (0.03)	0.36 (0.09)	0.35 (0.07)	0.35 (0.01)	
WHR	0.122 (0.05)	0.160 (0.02)	0.170 (0.04)	0.155 (0.04)	0.140 (0.02)	

Text-figure 11 shows a plot of all specimens on the second and third factor axes. With the exception of a single specimen, the *integra* and *marylandica* select groups do not overlap at all, and the *subcylindrica* and *quadrata* select groups are widely separated. Both of these separations are mainly along the third axis. The distribution of total groups is generally similar to that shown in Text-figure 10, except that total group 4, including the *quadrata* select group, is more divergent from the others. As in Text-figure 10, no unambiguous groups could be distinguished were they not identified *a priori*.

The rotated factor matrix (Table 6) reflects the pattern of covariation that determines the high or low projection of specimens on the factor axes (Hallam and Gould, 1975, p. 520). The first factor in this analysis is largely a size factor, dominated by shell, body whorl, and callus lengths, and shell widths. The two shouldering indices (**SH1** and **SH2**) score weakly negatively. The second axis is dominated by measures of spire height (**VSH**, **DSH**), with measures of spire angle (**AAN**, **PAN**) scoring moderately negatively. The two shouldering indices and pleural angle score by far the highest on the third axis, with most size measures (as well as apical angle) scoring negatively.

Discriminant Analysis.—Discriminant, or canonical

Table 6.—Varimax-rotated factor matrix for the first three factors in the morphometric analysis of *Bullia* (*Bulliopsis*) in this study. See Text-figure 9 for key to abbreviations of variables.

	factor 1	*factor 2*	*factor 3*
SHL	0.75074	0.16414	−0.07190
TSL	0.80113	0.23163	−0.07462
BWW	0.82948	0.26241	0.11853
TSW	0.85210	0.15475	0.08808
STH	0.82929	0.16483	0.05208
VSH	0.34079	0.75685	−0.02003
DSH	0.42143	0.76923	0.03290
APL	0.73846	0.15262	−0.10385
CAL	0.83746	0.04466	−0.14110
APW	0.57215	−0.02063	−0.21275
ACW	0.56776	−0.12432	−0.37420
SWH	0.21787	0.38491	0.14779
PAN	0.25941	−0.47566	0.66346
AAN	0.05377	−0.69981	−0.14700
SH1	−0.13084	0.20226	0.60734
SH2	−0.18684	0.28540	0.42894
percent of total variance	38.3	12.8	7.3

analysis differs in several respects from factor analysis. Factor analysis examines patterns of variation within a single sample in which no *a priori* subgroups have been designated. Discriminant analysis assumes that groups have been defined and assesses the multivariate differences among them. Text-figure 12 is a plot of all specimens in the plane of the first and second discriminant axes. The four select groups are clearly separated, with *quadrata* closest to *subcylindrica*. When the entire sample is considered, the four total groups are not separated out, although they clearly occupy different portions of the bivariate space.

Discussion

In light of the high degree of overlap displayed in the multivariate analyses, and the apparent abundance of morphological intermediates, it could be argued that these specimens actually comprise a single, highly variable biological species. Solely on the basis of Text-figures 10–12, there is insufficient information to allow delimitation of discrete morphologies which might be designated as specific-level taxa. Similar results were obtained by Kaesler (1970), studying the Permian fusulinid genus *Pseudoschwagerina* Dunbar and Skinner, 1936, "a group of fossils that are presumably related to each other phylogenetically and that include continuously evolving lineages" (Kaesler, 1970, p. 91). Four species, one with two subspecies, had previously been described, and Kaesler used a factor analysis similar to that employed here, plotting results of the first three factors on a pair of three-dimensional stereographs. No discrete clusters were distinguishable.

In neither Kaesler's foraminifera nor the present study, however, were taxonomic decisions themselves based on morphometric analyses of a series of co-occurring specimens. Rather taxa were designated subjectively beforehand on the basis of qualitative differences in morphology and stratigraphic distribution. In the present case, morphometric analyses serve as a test of this systematic hypothesis, and have been used to investigate the nature of variation within and among the designated taxa. Kaesler attributed his results to the combined effects of high variability at a single time within taxa and to evolutionary change within taxa through time. Raup and Stanley (1978, p. 97) have described his *a priori* groupings as "reasonable" in light of his factor analysis. In the case of *Bulliopsis*, I similarly believe there is justification for discriminating separate taxa from the splay of morphological variation.

Text-figures 10–12 suggest the following conclusions: (1) the four select groups are successfully discriminated by the morphological variables measured; (2) there is a great deal of variation within each of the four total groups around each corresponding select group; (3) the morphometric analyses describe much of the basic shape variation exhibited by the entire sample; and (4) only a very small number of specimens could not be assigned by eye to one of the four total groups: this contrasts somewhat with the degree of overlap evident in the multivariate plots, suggesting that not all of the morphological features that allow visual assignment were successfully quantified in this analysis.

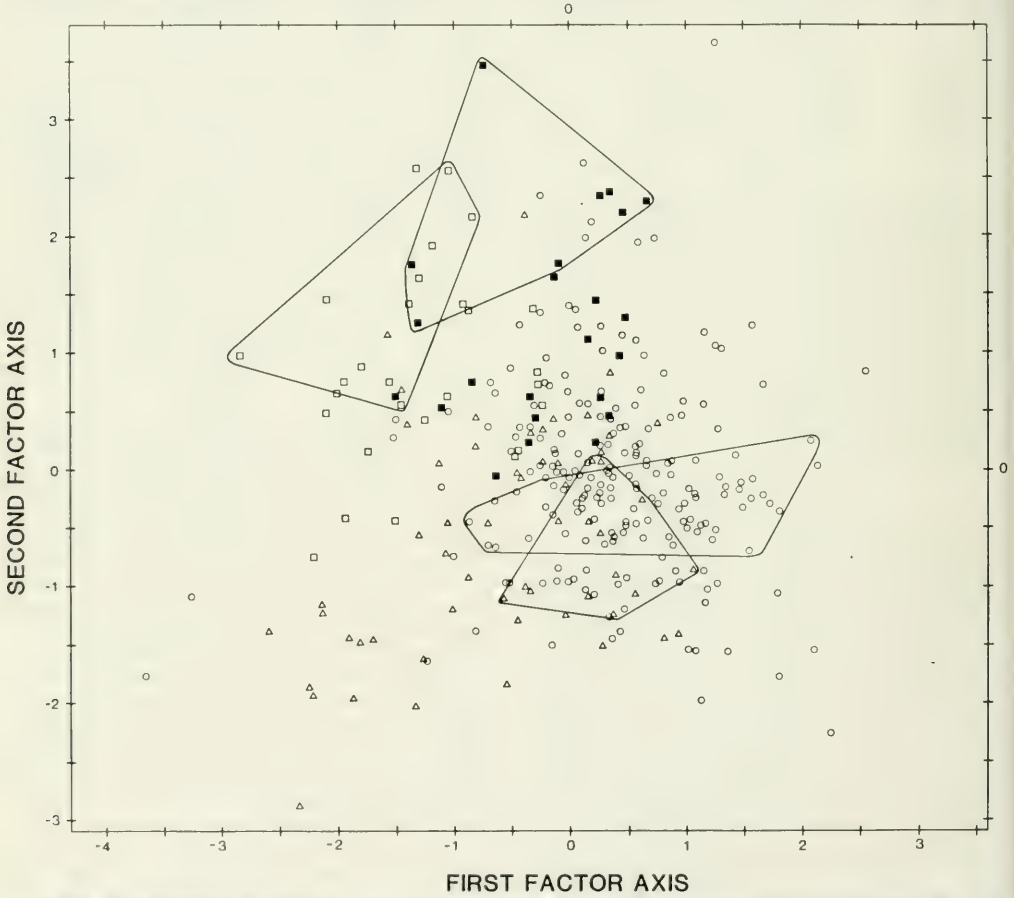
The total proportion of variance accounted for by the first three factors in the factor analysis is low. It takes 10 factors to account for 90% of the total variance. This pattern may be due to the very small range of size represented by the specimens measured; as there is little variation in size, the first factor, which is a size factor in most analyses, accounts for very little variance. It also suggests, however, an absence of well-defined pattern in the variation among individuals, and relatively low correlations between the variables measured (Reyment, 1985, p. 88). The latter is confirmed by the matrix of correlation coefficients (Table 7). This group of gastropods appears to have been relatively conservative in its morphology, with no population changing its basic form very dramatically. In his multivariate analysis of foraminifera, Kaesler (1970) similarly found that his first three factor axes explained only 55% of the total variance.

Variation in the morphological features measured may be examined in more detail by considering the distribution of specimens in the morphospace described by the factor axes. The four forms occupy different, if overlapping, regions. For example in Text-figure 10, 46% of total group 2 [= *marylandica*] spec-

imens fall in the fourth quadrant, while only 17% of total group 1 [= *integra*], and no specimens of total group 3 [= *subcylindrica* + *quadrata* from the Maryland St. Mary's] or total group 4 [= *quadrata* and *subcylindrica* from the Virginia Eastover] fall there. Forty-eight percent of total group 1 specimens fall in the third quadrant, while only about 13% of total group 2 and three individuals of total groups 3 and 4 combined fall there. Eighty-two percent of total group 3 individuals fall in the second quadrant while only 14% of total group 2 fall there. The method of dealing with missing values used by SPSS-X has, furthermore, probably contributed to the high degree of overlap. By substituting means calculated from the entire data matrix, this method reduces heterogeneity (and variance) within a data set.

Consideration of these specimens solely by means of an overall analysis, as if they all co-occurred in a single horizon, however, is misleading. As recognized in the initial description of the total groups, above, the designated taxa actually show a distinct pattern of temporal and geographic occurrence (Table 4; Text-fig. 13).

The sample from Little Cove Point (Text-fig. 15d) contains both typical *Bulliopsis marylandica* and *B. integra* in appreciable numbers, with *B. marylandica* by far the more abundant (Table 4). A small number of specimens referable to *B. subcylindrica* are also present. *Bulliopsis* is not abundant, but is relatively easy



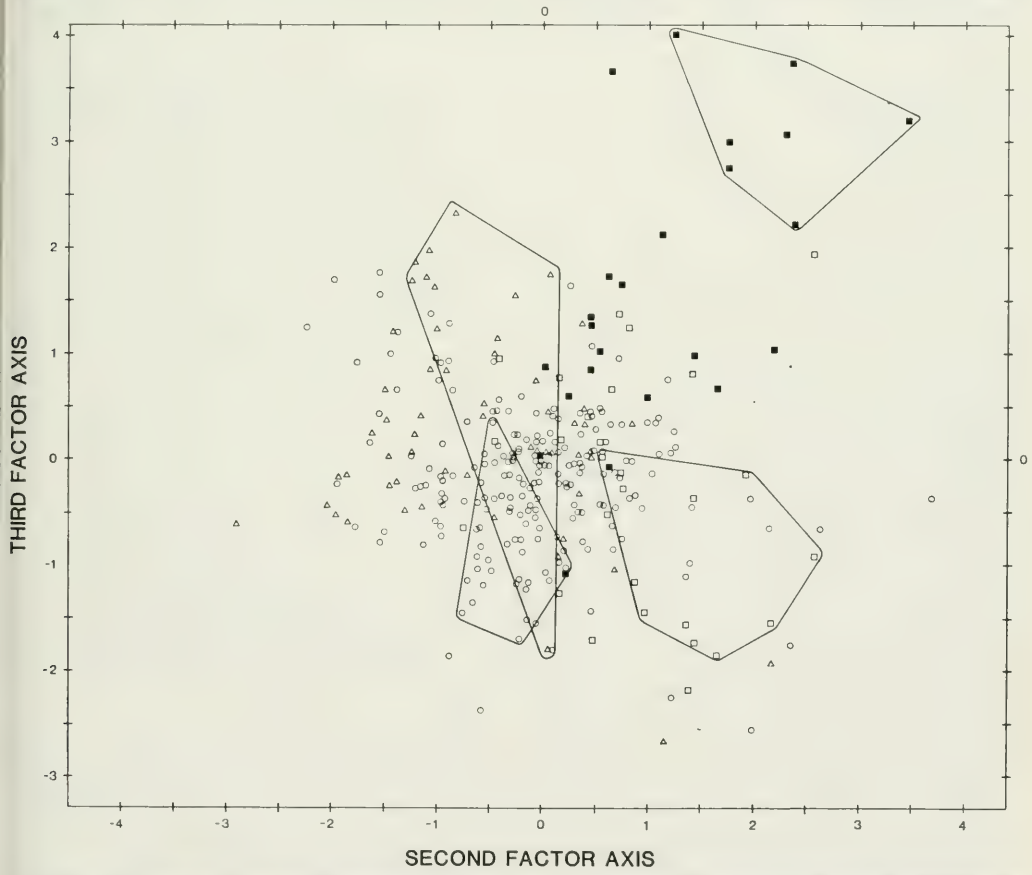
Text-figure 16.—Scatterplot of scores on the first two factor axes for all specimens of *Bulliopsis* collected from the Chesapeake Bay region for this study. The four select groups are outlined. △ = *integra* (total group 1); ○ = *marylandica* (total group 2); □ = *quadrata* + *subcylindrica* from Maryland St. Mary's (total group 3); ■ = Bowler's Wharf specimens (total group 4).

to find in the St. Mary's deposits exposed at Little Cove Point. Specimens were collected both *in situ* and from slumps along the cliffs. The specimens collected *in situ* in the high cliffs at Little Cove Point show no separation of taxa nor any changes in morphology with stratigraphic position.

Samples of *Bulliopsis* from Langley's Bluff and Deep Point (Text-fig. 15c) show some marked differences from those from Little Cove Point. Typical *B. marylandica* seems to have disappeared[9]. Typical *B. integra*, virtually identical to that represented at Little Cove Point, is still present. *B. quadrata sensu* Martin (1904) [= *subcylindrica* Conrad, 1866b], is well represented in samples from both Deep Point and Langley Bluff.

The shouldered morphotype, similar to Conrad's type specimens of *B. quadrata*, first appears in the beds at Deep Point. Conrad's specimens probably came from beds along the St. Mary's River, corresponding to either the "Deep Point" or "Windmill Point" horizons. Samples of *Bulliopsis* from Windmill Point and Deep Point are very similar (Text-figs. 15b, c). Typical *B. integra* is the most abundant form in the beds exposed at Windmill Point, followed by *B. subcylindrica*. Again the shouldered form is also present, in approximately the same proportions as in the Deep Point beds. In the material from Windmill Point (Text-fig. 15b), how-

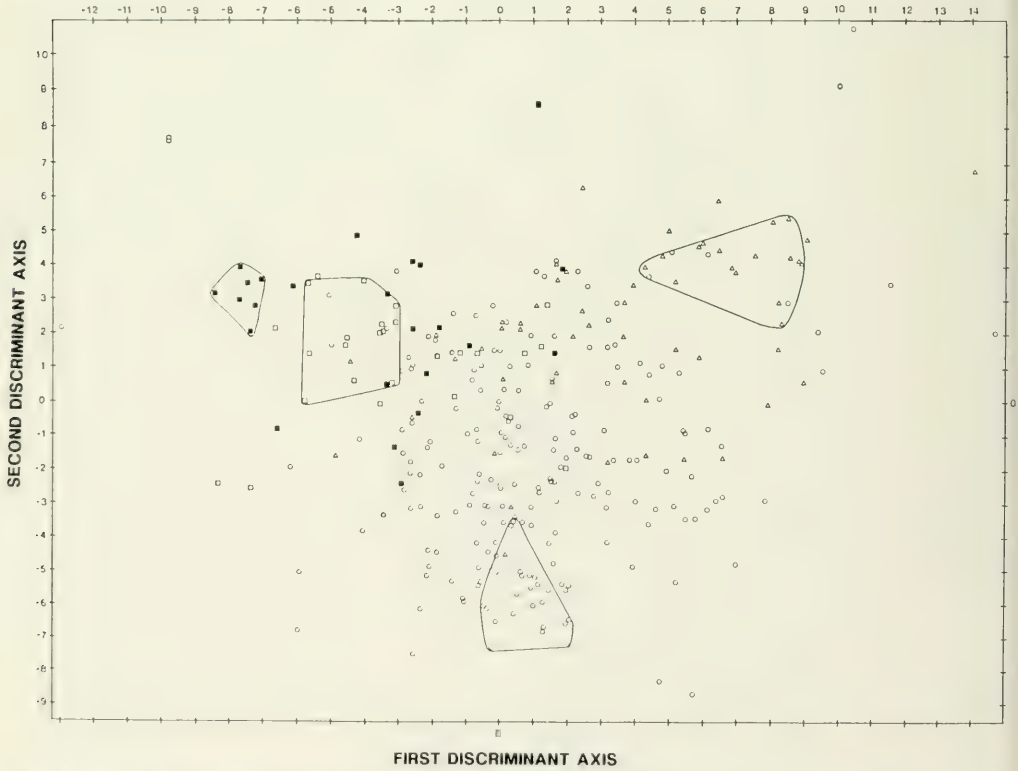
[9] It should be noted, however, that Martin (1904) listed the St. Mary's River as a locality for *B. marylandica*, but did not indicate exactly where. All sediments exposed here apparently post-date those at Little Cove Point.



Text-figure 11.—Scatterplot of scores on the second and third factor axes for all specimens of *Bulliopsis* collected from the Chesapeake Bay region for this study. The four select groups are outlined. △ = *integra* (total group 1); ○ = *marylandica* (total group 2); □ = *quadrata* + *subcylindrica* from Maryland St. Mary's (total group 3); ■ = Bowler's Wharf specimens (total group 4).

Table 7.—Correlation matrix for factor analysis of *Bulliopsis* specimens. See Text-figure 9 for key to abbreviations of variables.

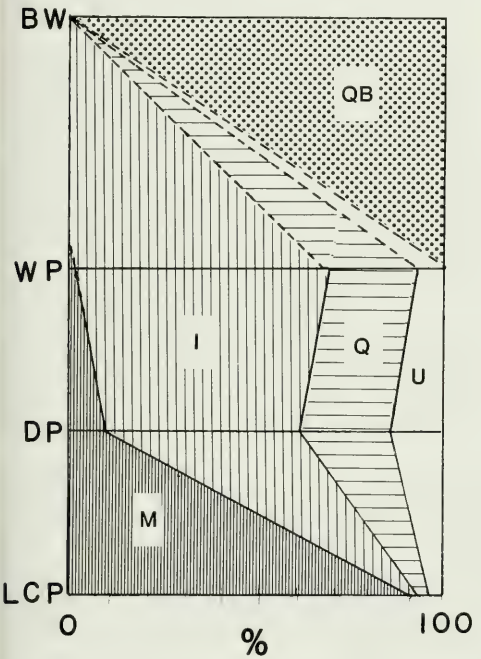
	SHL	*TSL*	*BWW*	*TSW*	*STH*	*VSH*	*DSH*	*APL*
SHL	1.00000							
TSL	0.56316	1.00000						
BWW	0.62332	0.63575	1.00000					
TSW	0.57705	0.71798	0.80310	1.00000				
STH	0.60418	0.60536	0.83146	0.73899	1.00000			
VSH	0.34883	0.43565	0.46251	0.40531	0.37361	1.00000		
DSH	0.43166	0.50412	0.57119	0.47263	0.43961	0.71478	1.00000	
APL	0.52002	0.65299	0.53435	0.56013	0.56155	0.36067	0.36792	1.00000
CAL	0.66695	0.68523	0.61558	0.65641	0.65181	0.25316	0.34746	0.68267
APW	0.33697	0.47696	0.37635	0.42879	0.38366	0.24033	0.21971	0.38642
ACW	0.45783	0.41613	0.30823	0.34888	0.37216	0.08219	0.09431	0.44461
SWH	0.26489	0.19487	0.28854	0.21010	0.23187	0.23706	0.34847	0.14441
PAN	0.02628	0.05627	0.12058	0.15125	0.09042	−0.16917	−0.15505	0.03624
AAN	−0.00516	−0.10870	−0.10558	−0.04987	−0.07606	−0.38755	−0.42481	−0.09592
SH1	−0.06969	−0.11170	−0.05244	−0.07573	−0.07227	0.05064	0.07533	−0.03806
SH2	−0.06549	−0.05285	−0.09967	−0.10018	−0.11490	0.11191	0.06739	−0.09935



Text-figure 12.—Scatterplot of scores on the first two discriminant axes for all specimens of *Bulliopsis* collected from the Chesapeake Bay region for this study. The four select groups are outlined. △ = *integra* (total group 1); ○ = *marylandica* (total group 2); □ = *quadrata* + *subcylindrica* from Maryland St. Mary's (total group 3); ■ = Bowler's Wharf specimens (total group 4).

Table 7.—Continued.

CAL	*APW*	*ACW*	*SWH*	*PAN*	*AAN*	*SH1*	*SH2*
1.00000							
0.44142	1.00000						
0.49104	0.37660	1.00000					
0.14331	0.02502	0.07563	1.00000				
0.06430	0.03366	−0.00072	−0.00676	1.00000			
−0.04880	0.06245	0.04618	−0.17036	0.11987	1.00000		
−0.13769	−0.08266	−0.18293	0.01611	0.05696	−0.19984	1.00000	
−0.15171	−0.12062	−0.15308	0.04370	−0.00104	−0.16437	0.18513	1.00000



Text-figure 13.—Proportional representation of the four *Bulliopsis* morphotypes at each of the four stratigraphic levels sampled in the Chesapeake Bay region. Vertical axis is stratigraphic order; horizontal axis is percent of all *Bulliopsis* found at that level. **BW** = Bowler's Wharf, loc. 6; **WP** = Windmill Point, loc. 3; **DP** = Deep Point, loc. 5; **LCP** = Little Cove Point, loc. 1; **M** = *marylandica*; **I** = *integra*; **Q** = *quadrata*; **QB** = *quadrata bowlerensis*; **U** = unidentified. Figure is based on data from only the four sampled levels, and data points representing these localities are connected by straight lines; actual abundances between these levels are unknown.

ever, it is possible to see an almost continuous gradation of morphology between that recognizable as *B. subcylindrica* and *B. quadrata*. Despite repeated efforts on my part, and the attempts of impartial volunteers, it proves impossible to assign consistently by eye all of the individuals from Windmill Point to one or the other discrete morphotype.

By the late Miocene, as represented by the samples from the Cobham Bay Member of the Eastover Formation at localities along the Rappahannock River in Virginia, the variety of morphologies within *Bulliopsis* had declined, and populations are dominated by large individuals of the shouldered morph. Typical *B. integra* does not appear to be present and is presumed to have become extinct prior to this time. The smoother morphotype, *B. subcylindrica*, which was relatively common lower in the section, has declined, and is represented only by a few small specimens. The sample from Bowler's Wharf, illustrated in Text-figure 15a, suggests an intergradation between the extreme, shouldered morphology and a form very similar to that assigned to *B. subcylindrica* at Windmill Point. This is clearly represented by the values of the shouldering indices through the stratigraphic section (Table 8).

Patterns of morphological transition through time are thus evident in *Bulliopsis* from the St. Mary's and Eastover formations. To investigate further the taxonomic and morphologic relationships of these forms, one would like to be able to analyze quantitatively populations of putative taxa co-occurring at a single locality. Sufficient samples are available, however, for only a single locality. Text-figure 16 shows a plot of scores on the first two factors for the 42 specimens of *integra* and the 20 specimens of *subcylindrica* + *quadrata* and intermediates collected at Windmill Point. The pattern is consistent with that which might be expected for two relatively closely related species. While

Table 8.—Means and standard deviations (in parentheses) for calculated shouldering indices for all taxa of *Bullia* (*Bulliopsis*) by locality. See Text-figure 9b for key to abbreviations of variables and method of index calculation. **LCP** = Little Cove Point, loc. 1; **DP** = Deep Point, loc. 5; **LB** = Langley's Bluff, loc. 2; **CP** = Chancellor's Point, loc. 4; **WP** = Windmill Point, loc. 3; **BW** = Bowler's Wharf, loc. 6. X = no sample; — = single specimen only.

	LCP	*DP*	*LB*	*CP*	*WP*	*BW*
marylandica						
SH1	1.06 (0.018)	X	1.08 (—)	X	X	X
SH2	1.04 (0.23)	X	1.04 (—)	X	X	X
integra						
SH1	1.06 (—)	1.06 (0.02)	X	X	1.06 (0.015)	X
SH2	X	1.02 (0.015)	X	X	1.02 (0.012)	X
quadrata						
SH1	1.07 (—)	1.09 (0.03)	X	1.07 (—)	1.07 (0.03)	X
SH2	1.08 (—)	1.03 (0.04)	X	1.06 (—)	1.06 (0.02)	X
quadrata bowlerensis						
SH1	X	X	X	X	X	1.1 (0.04)
SH2	X	X	X	X	X	1.1 (0.05)

there is substantial overlap, the mean values for each taxon fall outside the range of variation of values for the other.

Morphometric and stratigraphic approaches thus suggest that three, somewhat variable species-level taxa are distinguishable: *B. marylandica*, probably limited to the Little Cove Point Member of the St. Mary's Formation; *B. integra*, ranging throughout the St. Mary's; and *B. quadrata*, including all individuals agreeing with the types of *B. quadrata* (Conrad, 1830) and *B. subcylindrica* (Conrad, 1866b) from the "Deep Point" and "Windmill Point beds" of the St. Mary's Formation, as well as all specimens from the Cobham Bay Member of the Eastover Formation. *B. subcylindrica* and *B. quadrata* grade into one another in beds of the Windmill Point Member of the Maryland St. Mary's, with the *subcylindrica* morph predominant, and cannot be recognized as distinct, co-occurring species. *Bulliopsis* in the Eastover Formation of Virginia, dominated by the *quadrata* morph, appears to be the direct phyletic descendant of the polymorphic St. Mary's form. The morphological differences between *B. quadrata* in the Eastover and *B. quadrata* in the St. Mary's are, therefore, due to continuous phyletic evolution, rather than to change associated with a speciation event. This is represented at least partly by changes in the shouldering indices through time among species of *B. quadrata* s. l. (Text-fig. 17).

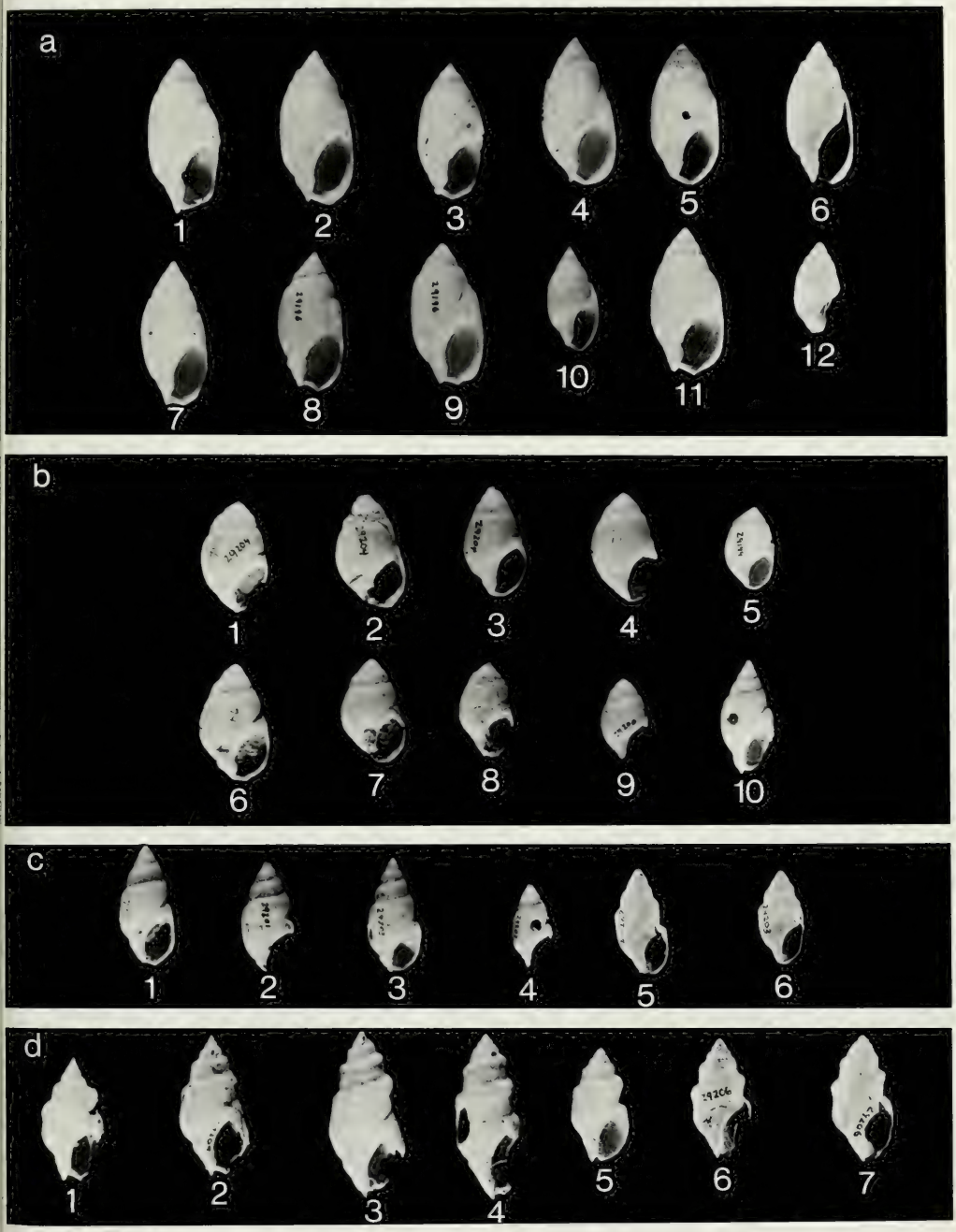
On the recognition of genetic polymorphism in fossil populations, Beerbower (1968, p. 82) has commented that:

> If the variant forms occur together in every reasonably sized sample then polymorphism is highly probable if not certain. The converse, however, is not true, for polymorphism varies in space or time.

This reasoning is consistent with the present example. With the exception of Little Cove Point, all localities yielding the *subcylindrica* morph also yield the *quadrata* morph, albeit in differing proportions. It seems plausible that the *Bulliopsis quadrata* lineage evolved through time by the gradual shift in frequency (and perhaps profundity of expression) of a structural polymorphism (Allmon, 1985).

The environments in which these gastropods lived almost certainly had important effects on their evolution, probably both indirectly through the establishment of varying selective regimes, and directly through ecophenotypic effects. As shown in Text-figure 7, species of *Bulliopsis* followed the shifting basins southward throughout the late Miocene, inhabiting what were probably the shallower areas on the northern edges, and being absent from deeper waters farther south. Suitable environments and conditions were probably available without major interruption during the time of the deposition of the St. Mary's Formation. At the end of this period, however, a major regression and

Text-figure 14.—The four "select groups" of specimens chosen to represent the four *Bulliopsis* morphotypes (all approx. ×1). **a.** *Bulliopsis marylandica* (Conrad, 1862a) from Little Cove Point, Calvert Co., Maryland: figs. 1–7, 11, 12, collectively numbered MCZ(IP) 29195; figs. 8–10 collectively numbered MCZ(IP) 29196. **b.** *Bulliopsis integra* (Conrad, 1842): figs. 1–4 from Windmill Point, St. Mary's Co., Maryland, MCZ(IP) 29204; fig. 5 from Langley's Bluff, St. Mary's Co., Maryland, MCZ(IP) 29202; fig. 7 from Little Cove Point, Calvert Co., Maryland, MCZ(IP) 29197; figs. 8, 9 from Windmill Point, St. Mary's Co., Maryland, MCZ(IP) 29205; figs. 6, 10 from Deep Point, St. Mary's Co., Maryland, MCZ(IP) 29200. **c.** *Bulliopsis quadrata* (Conrad, 1830): fig. 1, from Langley's Bluff, St. Mary's Co., Maryland, MCZ(IP) 29199; figs. 2, 4–6 from Windmill Point, St. Mary's Co., Maryland, MCZ(IP) 29203; fig. 3 from Deep Point, St. Mary's Co., Maryland, MCZ(IP) 29201. **d.** *Bulliopsis quadrata bowlerensis*, n. subsp., from Bowler's Wharf, Essex Co., Virginia: fig. 1, MCZ(IP) 29207 [paratype]; fig. 2, MCZ(IP) 29209 [paratype]; fig. 3, MCZ(IP) 29208 [holotype]; figs. 4–7 are figured specimens, collectively numbered MCZ(IP) 29206.


a
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4
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11
12
b
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c
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d
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6
7

drop in temperatures had profound effects on mollusk faunas of the region (Ward and Blackwelder, 1980; Ward, 1980; Ward, 1985; Ward, *in press*). *Bulliopsis* is not known from the Claremont Manor Member of the Eastover Formation. In the overlying Cobham Bay Member, its occurrence is restricted to a relatively small area, again on the northern margin of the basin, around what is now the Rappahannock River. The sediments exposed in the vicinity of Bowler's Wharf were apparently deposited in a relatively quiet embayment formed by an underlying structural feature (Ward and Blackwelder, 1980, p. 27; Ward and Strickland, 1985).

Conditions, therefore, may have existed both for significant selective and direct ecophenotypic influences on later representatives of *Bulliopsis*. The time interval between the deposition of the "Windmill Point" and Cobham Bay units may have been one of considerable extrinsic stress for these gastropods, and may have caused not only the extinction of one or more species, but also morphological changes in the species that survived. The environmental conditions represented by sediments at Bowler's Wharf are different enough from the shelly sands of the "Windmill Point beds" to suggest that at least some of the morphological differences evident between the *Bulliopsis* of these horizons may have been ecophenotypic. Slight modifications of external sculpture, proportion, and size seem likely candidates for such effects. The exact role of environment in effecting these morphological changes is difficult to assess. That it was not solely responsible is suggested by the co-occurrence of smooth and shouldered morphs in the upper St. Mary's Formation.

The determination of biological species solely from fossil material is always difficult. It is conventional practice, however, when analysis of the fossils themselves has been exhausted, to turn to examination of extant relatives. This is especially easy to do in the case of Cenozoic mollusks. Explaining such an attempt, Waller (1969, p. 8) writes:

> The degree of interspecific and intraspecific variation that may be expected among fossil species must be deduced, whenever possible, from the patterns of variation displayed by closely related living species and by the local populations that comprise them.

It is possible to make a similar analogy between *Bullia* (*Buccinanops*) *cochlidia* (Dillwyn, 1817), living today off the coast of southeastern South America, and fossil *Bulliopsis* from the mid-Atlantic Miocene. For the reasons summarized on pp. 24, 25, these living forms probably all belong to a single, morphologically variable species. *Bulliopsis* from the mid-Atlantic Miocene of the U. S. and this Recent species of *Buccinanops* are morphologically quite similar (compare Pls. 3, 7). If these shouldered and unshouldered forms of *Buccinanops* are held to belong to a single species, then *Bulliopsis quadrata* may be treated in a similar manner.

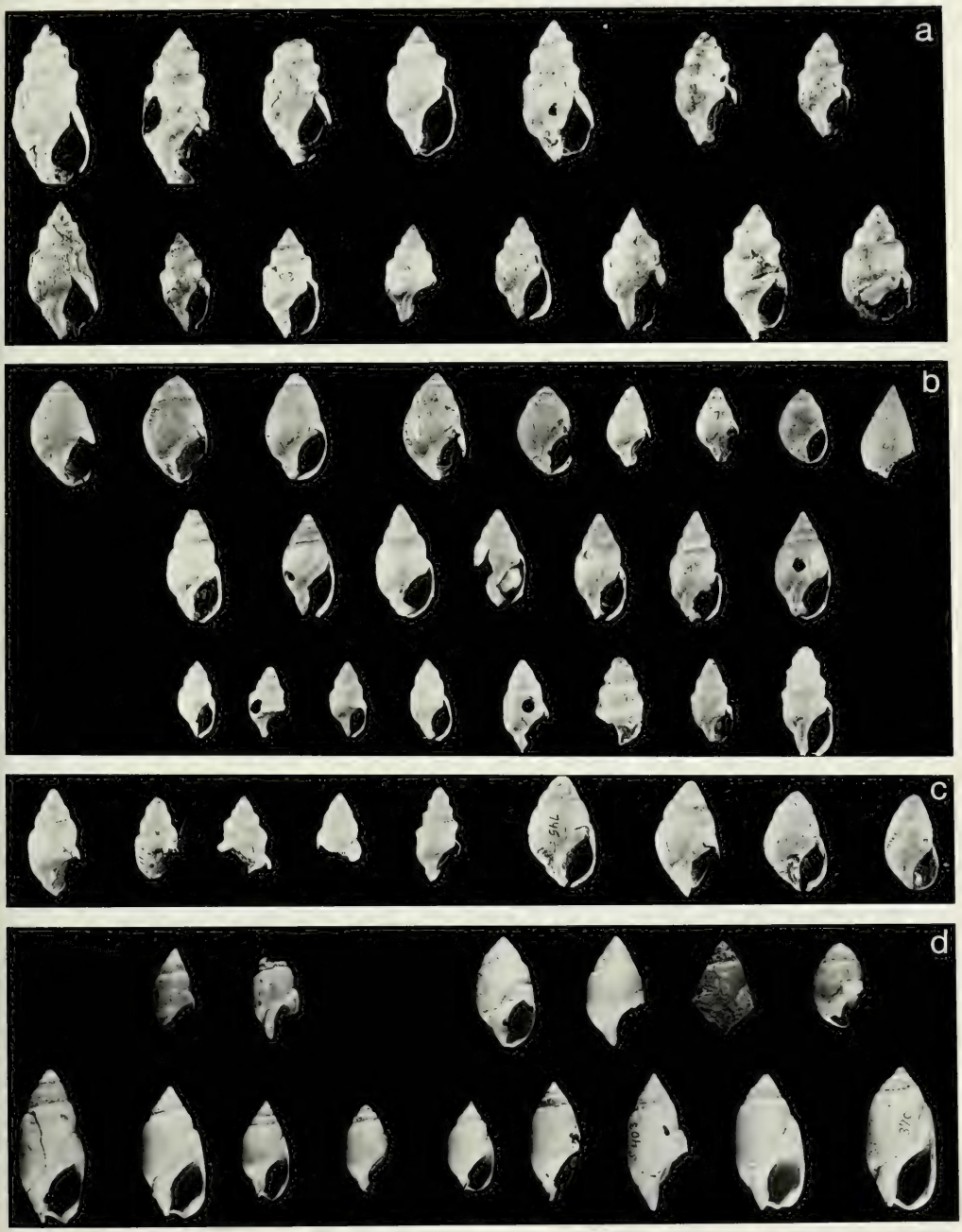
Form of the Shell Apex

When studying gastropod protoconchs, it is normally preferable to examine very small specimens, as these have the best chance of being well preserved. Few juvenile specimens of *Bulliopsis* have ever been found, however, and examination of shell apices had to be done on relatively large specimens.

Plate 8 shows scanning electron micrographs of the apices of specimens of *B. marylandica* from Little Cove Point and *B. quadrata* from Bowler's Wharf. Specimens chosen were the best preserved available, but all were relatively large. The specimens of *marylandica* appear to be better preserved than those of Bowler's Wharf specimens. They show no obvious breaks that might be interpretable as boundaries between P1 and P2 or P2 and the teleoconch. Spiral sculpture appears to begin on about the second whorl. If it is assumed that these specimens show well preserved apices, they suggest protoconch diameters of approximately 0.8–0.9 mm.

As an attempt to check whether or not these specimens do in fact represent actual shell apices and not broken, filled, and worn teleoconchs, I measured the minimum apparent diameter on 20 other specimens of *marylandica* through a light microscope at a magnification of 50×. These specimens varied in quality of preservation from obviously broken with unfilled holes in the apex to apparently relatively well preserved, and in total shell height from 0.4 to 1.1 mm. If size and relative state of preservation seems to have

Text-figure 15.—Representative samples of *Bulliopsis* from four stratigraphic levels in the upper Miocene of Maryland and Virginia (all approx. ×0.9). **a**. Representative sample of *Bulliopsis* from the Cobham Bay Member of the Eastover Formation, exposed along the Rappahannock River in the vicinity of Bowler's Wharf, Essex Co., Virginia. All specimens are assignable to a broadly defined *B. quadrata* but show variation from the smooth morph illustrated by Martin to the larger, shouldered morph. **b**. Representative sample of *Bulliopsis* from the Windmill Point Member of the St. Mary's Formation, exposed at Windmill Point, St. Mary's River, St. Mary's Co., Maryland. Top row, *B. integra*; second row, *B. quadrata* (smooth *subcylindrica* form); bottom row, *B. quadrata*, varying from smooth on the left to shouldered on the right. **c**. Representative sample of *Bulliopsis* from the upper Little Cove Point Member of the St. Mary's Formation, exposed at Deep Point, St. Mary's River, St. Mary's Co., Maryland. Right four specimens, *B. integra*; left five specimens, *B. quadrata*, varying from the smoother *subcylindrica* form on the far left to the more shouldered *quadrata* s. s. form to the right. **d**. Representative sample of *Bulliopsis* from the lower Little Cove Point Member of the St. Mary's Formation, exposed at Little Cove Point, Calvert Co., Maryland. Top row: left two specimens, *B. quadrata* (*subcylindrica* form); right four specimens, *B. integra*. Bottom row: *B. marylandica*.


a
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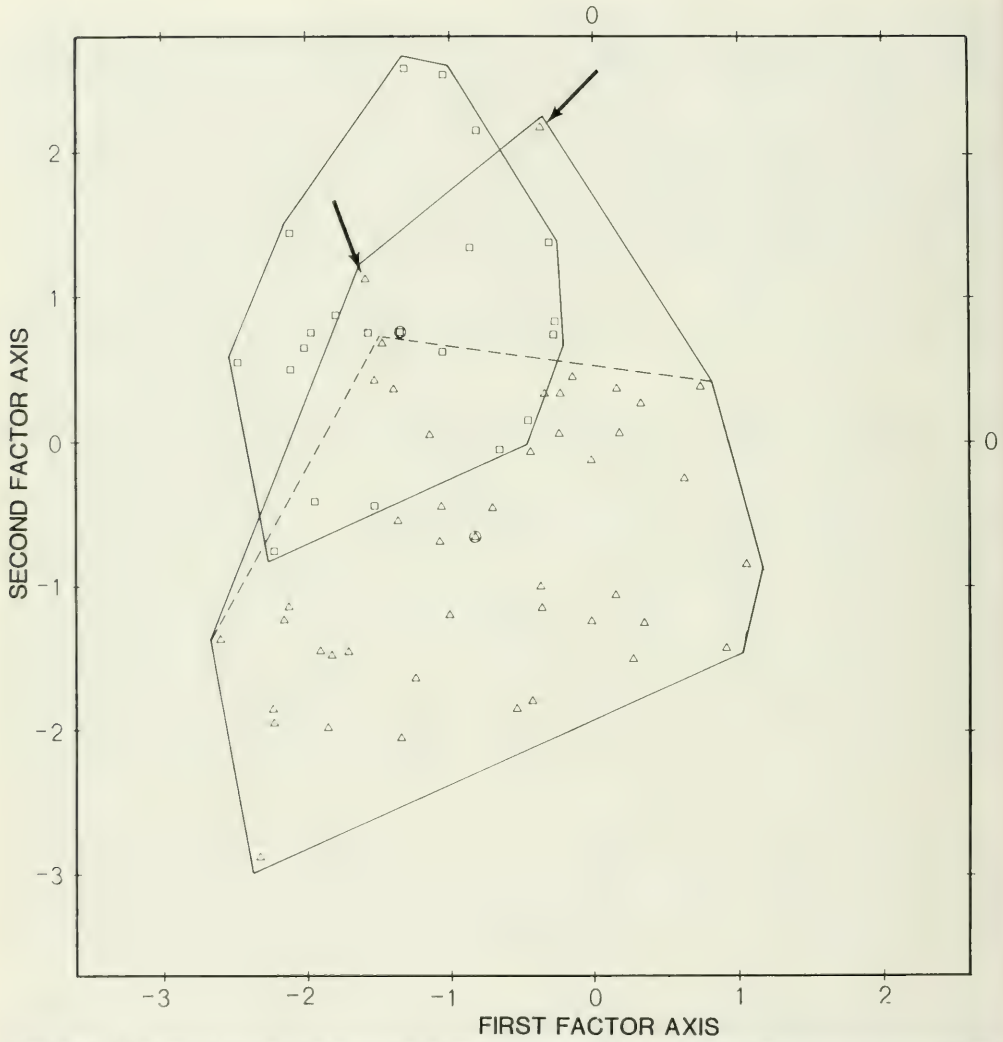
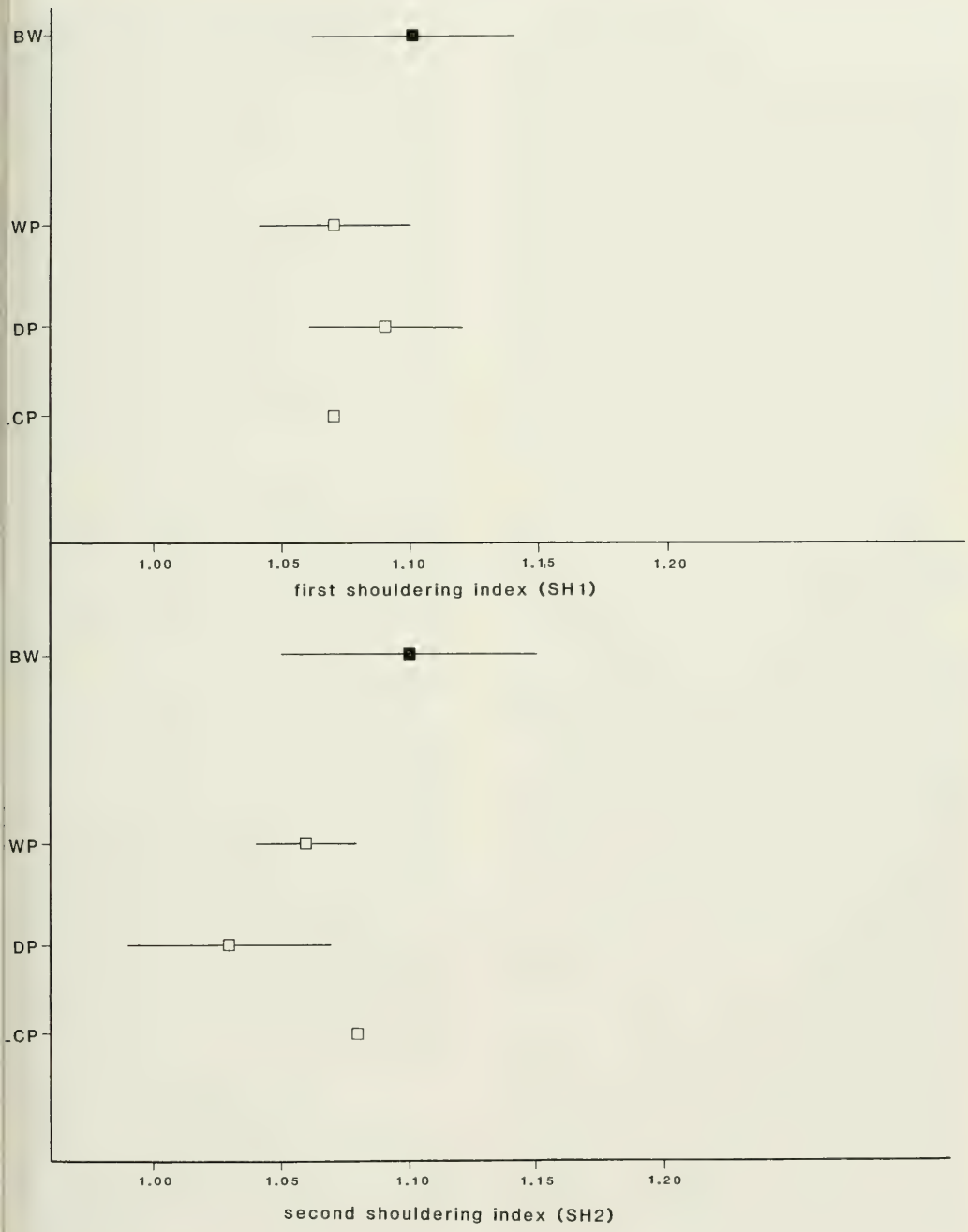


Text-figure 16.—Scatterplot of scores on the first two factor axes for specimens of *Bulliopsis integra* and *Bulliopsis quadrata* from Windmill Point, St. Mary's Co., Maryland. △ = *integra* (total group 1); □ = *quadrata* + *subcylindrica* (total group 3). Arrows indicate two specimens of *integra* which are more high-spired than normal. These two specimens are illustrated in Text-figure 15b [top row, first and fourth from the right]. Circled symbols are mean values for the two species.

little or no effect on measured apparent apex diameter, then this would increase confidence that the seemingly well-preserved specimens in Plate 8 actually represent shell apices[10]. The measured values ranged from 0.4

[10] I am grateful to K. P. Sebens of Northeastern University for this suggestion.

Text-figure 17.—Plots of mean values for the two calculated shouldering indices (see Text-fig. 9B) for all specimens of *Bulliopsis quadrata* from the four stratigraphic horizons sampled in the Chesapeake Bay region. Squares mark positions of means; horizontal bars span ± two standard deviations. □ = *Bulliopsis quadrata* s. s.; ■ = *Bulliopsis quadrata bowlerensis*, n. subsp. **BW** = Bowler's Wharf, loc. 6; **WP** = Windmill Point, loc. 3; **DP** = Deep Point, loc. 5; **LCP** = Little Cove Point, loc. 1. Only a single specimen from Little Cove Point was measured.


BW
WP
DP
CP
1.00
1.05
1.10
1.15
1.20
first shouldering index (SH1)
BW
WP
DP
CP
1.00
1.05
1.10
1.15
1.20
second shouldering index (SH2)

to 0.8 cm, suggesting that, to a rough approximation, the values measured from Plate 8 may be reliable.

The specimens of *quadrata* from the Rappahannock are more difficult to interpret. They are clearly eroded to some degree, although it is again difficult to tell just how much. Apparent diameters of these apices range from 0.4–0.8 mm, with at least one specimen showing a significantly more acute apex than the others.

All apparent diameters measured on these specimens fall well within the ranges suggested by Jablonski and Lutz (1983) for nonplanktotrophic species. Although, in the absence of juvenile specimens, there is no way to be sure that these dimensions actually represent protoconch diameters, the consistency of the apparent dimensions suggests that they are approximately correct. The apical profiles also seem consistent with the interpretation that the species of *Bulliopsis* were nonplanktotrophic. This conclusion can only be considered tentative in light of the uncertain relationship (discussed on pp. 17–19) between protoconch form and developmental mode in living *Bullia* group species.

Bulliopsis *from New Jersey*

Specimens referable to *Bulliopsis* are known outside of Maryland and Virginia only from well borings in southern New Jersey. Richards (1947) and Gardner (1948b) discuss specimens of *B. integra* and *B. quadrata* from deep wells in Maryland and New Jersey.

In 1894, Whitfield described the species *Buccinanops variabilis* from specimens obtained from a well boring at Cape May, New Jersey. He wrote that he had at first "been inclined to consider this shell identical with Mr. Conrad's *Bulliopsis quadrata*" (Whitfield, 1894, p. 107). Martin (1904, pp. 197–198) claimed that these specimens "do not differ at all from young of *B. integra* from the Maryland localities". Richards and Harbison (1942) agreed with this synonymy. The Kirkwood Formation is now generally believed to correlate with the lowermost part of the Calvert Formation in Maryland and Virginia (Isphording, 1970; Gibson, 1983; Ward, 1980; Ward, 1985; Ward, *in press*), and the beds containing *Bulliopsis variabilis* are probably equivalent to beds 2 and 3A of Shattuck (1904) [Ward, oral commun., 1987; Ward, *in press*). Thus, at least one species of *Bulliopsis* dates from as early as the early Miocene in the Mid-Atlantic coastal plain.

Morphologically, the specimens described by Whitfield are intermediate between the inflated *Bulliopsis integra* and the more elongate *B. marylandica* typical of the Maryland St. Mary's (see Pl. 7, figs. 18–22). The callus is thin and inconspicuous, as in typical *B. integra*. While smaller specimens show a very inflated body whorl and short attenuated spire, larger individuals often have decidedly straight-sided body whorls. The New Jersey specimens are much smaller than averages for Maryland or Virginia forms, none measuring more than 15 mm total height.

It is reasonable to suggest that *Bulliopsis variabilis* is close to the common ancestral form of later *Bulliopsis* species from Maryland and Virginia, particularly *marylandica* and *integra* which it most resembles.

Systematic Summary

I have proposed on pp. 20–27 (see also p. 115) that living South American species usually referred to the genus *Buccinanops* d'Orbigny, 1841 be included in the genus *Bullia* Gray, 1834. So close is the morphological resemblance of Mid-Atlantic Miocene species of *Bulliopsis* Conrad, 1862a to some of these living South American species that, if they occurred together as living or fossil forms, it might be reasonable to treat them as congeneric, the major differences between them being those of size and robustness. There is thus justification for including the species of *Bulliopsis* within *Buccinanops*.

It seems more useful, however, to retain the name *Bulliopsis*. It is a name long used for these Miocene species in the biostratigraphic literature (*e.g.*, Gardner, 1948b), and the species are furthermore the only representatives of the group in this part of the stratigraphic column in the eastern U. S., and so are somewhat isolated geographically. I, therefore, return *Bulliopsis* to its original taxonomic position (Conrad, 1862a) as a subgenus within the genus *Bullia*.

Genus **BULLIA** Gray *in* Griffith and Pidgeon, 1834

Subgenus **BULLIOPSIS** Conrad, 1862a

Type Species (by original designation).—*B.* (*B.*) *quadrata* (Conrad, 1830).

Diagnosis.—Shell ovoid, medium-sized for genus, 10–30 mm adult total height. Spire relatively short, comprising one-fourth to one-third of total height. Aperture ovoid, lacking marked posterior canal, usually comprising one-third to one-half total shell height. Anterior canal short, wide and moderately deep. Outer lip of aperture simple. Parietal callus always present but variable in extent and thickness. Anterior end of columella bears weak terminal fold; external sculpture ranges from faint growth lines to pronounced subsutural carinae and shouldering and conspicuous growth lines.

Bullia (Bulliopsis) integra (Conrad)
Plate 7, figure 2

Buccinum integrum Conrad, 1842, p. 194, pl. 2, fig. 5.
? *Buccinum pusillum* Lea, 1843, p. 165 (list only); Lea, 1846, p. 272, pl. 37, fig. 98.
Bullia (*Bulliopsis*) *ovata* Conrad, 1862a, p. 287.
Tritia (*Bulliopsis*) *integra* (Conrad). Conrad, 1862b, p. 562; Meek, 1867, p. 20.

Tritia (*Bulliopsis*) *ovata* (Conrad). Conrad, 1862b, p. 562; Meek, 1867, p. 20.
Nassa (*Bulliopsis*) *integra* (Conrad). Conrad, 1866b, p. 66, pl. 3, fig. 5.
Nassa (*Bulliopsis*) *integra* var. *ovata* Conrad, 1866b, p. 66, pl. 3, fig. 4.
Melanopsis integra (Conrad). Conrad, 1868, p. 259.
Bulliopsis integra (Conrad). Martin, 1904, p. 197, pl. 50, figs. 1, 2; Moore, Lalicker, and Fischer, 1952, pp. 325–326, fig. 8-39(14); Vokes, 1957, p. 32.

Occurrence.—Maryland, St. Mary's County, St. Mary's River, Deep Point, Windmill Point, Chancellor's Point; Calvert County, Little Cove Point, Langley's Bluff; St. Mary's Formation, middle Miocene.

Range.—Upper middle Miocene.

Type locality.—"St. Mary's River and Calvert Cliffs, near mouth of Patuxent river" (Conrad, 1842) [probably = Little Cove Point, Calvert County, Maryland].

Types.—ANSP 15688 [six syntypes]; USNM 353123 [hypotype of Martin, 1904].

Other material examined.—Non-type material MCZ(IP) 29197, 29202, 29204; unnumbered specimens in the stratigraphic collections of the USGS; unnumbered CMM specimens [total: 135 specimens].

Description.—Medium-sized for subgenus, not exceeding 25 mm total height. Whorls number six to seven. Spire relatively short, penultimate and body whorl relatively large and inflated. Whorl profiles smooth and evenly rounded; external sculpture wholly lacking. Protoconch unknown. Callus reduced in thickness and extent compared to *B. marylandica*, scarcely extending out of aperture onto body whorl. Anterior end of columella simple, bearing only slight terminal fold. Anterior end of outer apertural lip not extending beyond end of columella. Aperture approximately one-and-one-half times as long as wide.

Bullia (Bulliopsis) marylandica Conrad
Plate 7, figure 1; Plate 8, figures 1, 2

Bullia (*Bulliopsis*) *marylandica* Conrad, 1862a, p. 287.
Tritia (*Bulliopsis*) *marylandica* (Conrad). Conrad, 1862b, p. 562; Meek, 1867, p. 20.
Nassa (*Bulliopsis*) *Marylandica* (Conrad). Conrad, 1866b, p. 65, pl. 3, fig. 3.
Melanopsis marylandica (Conrad). Conrad, 1868, p. 259.
Bulliopsis Marylandica (Conrad). Martin, 1904, pp. 198–199, pl. 50, fig. 4; Vokes, 1957, p. 32.

Occurrence.—Maryland, Calvert County, Little Cove Point; St. Mary's County, St. Mary's R. (?); St. Mary's Formation, middle Miocene.

Range.—Upper middle Miocene.

Type locality.—The locality given by Conrad (1862a) of St. Mary's County, Maryland is probably in error; the locality of the lectotype is Little Cove Point, Calvert County, Maryland.

Types.—Conrad's holotype lost [*fide* Moore, 1962]; Martin's figured specimen [USNM 353125: here designated lectotype].

Other material examined.—Non-type material MCZ(IP) 29195, 29196; unnumbered specimens in the stratigraphic collections of the USGS; unnumbered CMM specimens [total: 330 specimens].

Description.—Large for subgenus, up to 30 mm total height, most 20–25 mm. Whorls number seven to nine. Spire relatively short, body whorl large and rounded but not extremely inflated. Protoconch large and paucispiral, consisting of approximately two to two-and-one-half smooth whorls. External shell sculpture and shouldering lacking; shell profile evenly rounded and convex. Parietal callus well-developed and usually extending posteriorly onto body whorl from the aperture to approximately halfway between the posterior point of aperture and the suture. Periphery of callus on surface of body whorl is usually concave and may be chipped. Terminal columellar fold pronounced. Anterior canal well-developed, wide and deep.

Bullia (Bulliopsis) quadrata (Conrad)
Plate 7, figures 3–10

Nassa quadrata Conrad, 1830, p. 211, pl. 9, fig. 16.
Buccinum quadratum (Conrad). Conrad, 1842, p. 187.
Bullia (*Bulliopsis*) *quadrata* (Conrad). Conrad, 1862a, p. 287.
Tritia (*Bulliopsis*) *quadrata* (Conrad). Conrad, 1862b, p. 563; Meek, 1867, p. 20.
Nassa (*Bulliopsis*) *quadrata* Conrad, 1866b, p. 65, pl. 3, fig. 1.
Nassa (*Bulliopsis*) *subcylindrica* Conrad, 1866b, p. 66.
Melanopsis quadrata (Conrad). Conrad, 1868, p. 259; Richards, 1947, p. 28, pl. 11, fig. 6.
Bulliopsis quadrata (Conrad). Martin, 1904, p. 198, pl. 50, fig. 3; Gardner, 1948b, p. 116, pl. 1, fig. 27; Vokes, 1957, p. 32.

Occurrence.—Maryland, St. Mary's County, St. Mary's River, Windmill Point, Chancellor Point, Deep Point; Calvert County, Langley's Bluff; St. Mary's Formation, middle Miocene (*quadrata* s. s.); Eastover Formation, upper Miocene (*quadrata* subsp.)

Range.—Upper middle–middle upper Miocene.

Type locality.—Conrad (1830) listed the St. Mary's River, St. Mary's County, Maryland as the type locality; this species is most common at Windmill Point, west bank of St. Mary's River, opposite and southwest of St. Mary's City, St. Mary's County, Maryland (USGS loc. 25304), and this may have been the exact locality.

Types.—ANSP 15686 [four probable syntypes of *quadrata* Conrad, 1830]; ANSP 15687 [five probable syntypes of *subcylindrica* Conrad, 1866b]; USNM 353124 [hypotype of Martin, 1904].

Other material examined.—Non-type material MCZ(IP) 29194, 29198, 29201, 29203; unnumbered specimens in the stratigraphic collections of the USGS [total: 35 specimens].

Description.—Medium-sized to large for subgenus, up to 30 mm total height, most approximately 20 mm.

Spire relatively high; whorls usually straight-sided. Shell surface in *quadrata* s. s. smooth. Callus usually thick, periphery on the body whorl usually convex. Aperture relatively smaller and narrower than in other species. Anterior siphonal canal well-developed, deep and wide. Anterior point of outer apertural lip frequently attenuated and sharp. Terminal columellar fold distinct.

Bullia (Bulliopsis) quadrata bowlerensis,
new subspecies
Plate 7, figures 11–12; Plate 8, figures 3, 4

Bulliopis [*sic*] *quadrata* (Conrad). Ward and Blackwelder, 1980, p. 28.

Occurrence.—Virginia, Essex County, Rappahannock River, Bowler's Wharf, Union Mill, Layton's Landing; Eastover Formation, Cobham Bay Member, upper Miocene.

Range.—Middle upper Miocene.

Type locality.—Bowler's Wharf, Rappahannock River, Essex County, Virginia.

Types.—Holotype, MCZ(IP) 29208; Paratypes, MCZ(IP) 29207, 29209, USNM 434942, 434943, 434944 (Bowler's Wharf, Virginia), 434945 (four miles below Bowler's Wharf, Virginia), 434946 (1.5 miles east of Warsaw, Richmond County, Virginia).

Other material examined.—Topotypes MCZ(IP) 29206, non-type material, unnumbered specimens in the stratigraphic collections of the USGS (from Union Mill, VA) [total: 30 specimens].

Diagnosis.—Large to very large for subgenus; largest specimens up to 35 mm total height. Adapical margins of body and late spire whorls bear prominent carinae and subsutural shoulders. Whorl walls straight or only slightly convex; body whorl may be narrower beneath shoulder. Spire relatively elongate. Growth lines usually pronounced.

Description.—Shell elongate, relatively high-spired for subgenus, turbinate. Spire up to one-third total height. Whorls usually straight-sided, but may be slightly inflated and rounded abapically. Sutures deeply impressed. Abapical ends of body and spire whorls bear rounded constrictions, prominent but rounded carinae, and distinct, often horizontal shelves. Juveniles may display incipient beading in anticipation of carinae. Spire whorls elongate, usually five to six in number. Aperture less than one-half total height, generally leaf-shaped, elliptical, at least twice as long as wide. Very narrow posterior slit usually present. Siphonal canal short but wide and deep. Parietal callus thick, rounded at periphery; usually even with posterior end of aperture. Whorls usually marked by distinct growth lines which in very large specimens approach rough axial ribs in character.

Remarks.—This subspecies is distinguished by the overall distribution of morphologies displayed by the populations comprising it. The type specimens of *Bulliopsis quadrata* (Conrad, 1830) are not representative of the populations from which they were taken, but represented only one extreme of a morphological continuum dominated numerically by smaller, smoother individuals. Populations of *B. quadrata* from the upper Eastover Formation of Virginia, on the other hand, are dominated by larger, more sculptured forms. This occurs after the extinction or decline in abundance of all other morphologies in a geographic and ecologically restricted area. This situation corresponds to that suggested by Newell (1947) and Gould (1969) as justifying designation of a chronological subspecies.

Bullia (Bulliopsis) variabilis (Whitfield)
Plate 7, figures 18–22

Buccinanops variabilis Whitfield, 1894, pp. 107–108, pl. 17, figs. 13–18.

Bulliopsis integra (Conrad) [in part]. Martin, 1904, p. 197; Richards and Harbison, 1942, p. 215, pl. 21, figs. 7, 8 [*non integra* Conrad, 1842].

Occurrence.—New Jersey (subsurface), Kirkwood Formation.

Range.—Middle Miocene.

Type locality.—Well at Cape May, New Jersey, depth of 320–350' (Whitfield, 1894).

Material examined.—Syntypes, NJSM 10409; hypotypes, ANSP 14478, 15685 [total: 21 specimens].

Description.—Very small for subgenus, not exceeding 10 mm total height. Overall form somewhat variable; spire comprises one-fifth to one-third total height, often deformed with apex bent to one side. Body whorl straight-sided to evenly convex in profile, frequently widest just below the suture and narrowing continuously abapically to the anterior canal. Aperture never greater than one-half total height, usually twice as long as wide. Most specimens show pronounced terminal columellar fold. Parietal callus noticeable but not extending very far out of aperture over body whorl. Posterior slit never pronounced but often present. External shell sculpture lacking.

Remarks.—Although *variabilis* generally resembles *B. integra* in its frequently rounded and inflated body whorl and relatively short spire, true to its name it is highly variable in these characters. The sample available in the collections of the New Jersey State Museum and the Philadelphia Academy of Natural Sciences is virtually unimodal for total height at approximately 10 mm, much smaller than the mean size for any of the species of *Bulliopsis* from Maryland and Virginia.

CRETACEOUS OF THE SOUTHEASTERN U. S.

In his treatment of the gastropods of the Upper Cretaceous (upper Campanian–Maestrichtian) beds of Tennessee and Mississippi, Sohl (1964) describes sev-

eral species of the genus *Buccinopsis* Conrad, 1857 (Pl. 9, figs. 16, 17). Although Sohl includes *Buccinopsis* in the family Buccinidae, Nuttall (written commun., 1985; see also Taylor, Morris, and Taylor, 1980, p. 387, fig. caption citing Nuttall, pers. commun.; Taylor, Morris, and Taylor, 1980, cited by Sepkoski, 1982, p. 29) considers *Buccinopsis* to be the earliest known representative of Nassariidae, mainly on the basis of its pronounced terminal columellar fold (see Pl. 9, figs. 16, 17).

The earliest known occurrence of *Buccinopsis* is apparently an undescribed species from the uppermost Eutaw Formation (upper Santonian–lower Campanian) of Alabama [USGS loc. 27065] (Sohl, 1964). "As known," Sohl (1964, p. 188) concludes, "*Buccinopsis* is restricted to the Gulf and Atlantic coastal plains and ranges through the *Exogyra ponderosa* and *E. costata* zones (Santonian? to Maestrichtian)." Jablonski (1979) has presented stratigraphic and geographic range data for all previously recognized species of *Buccinopsis* as well as several forms he believes to be undescribed species. Dockery (oral commun., 1985) also believes that several undescribed species exist in the Coffee Sand and Coon Creek beds (Upper Cretaceous) of Mississippi.

Several points are important in evaluating species of *Buccinopsis* as possible ancestral taxa for the *Bullia* group and other nassariids: (1) The probability of *Buccinopsis* actually being among the earliest nassariids depends on the importance placed on the terminal columellar fold as a distinguishing character of the family. This feature is well-developed in all species of *Buccinopsis*, but if the terminal fold proves to be highly homoplastic among unrelated neogastropod stocks, this would make a definite relationship of *Buccinopsis* with later nassariids more difficult to support; (2) in general shell shape there is nothing to exclude *Buccinopsis* from an ancestral position, although the spires of species in this genus are relatively much shorter, and the anterior canals much longer, than in most later nassariids; (3) sculpture patterns are conspicuous but variable among species of *Buccinopsis*. Both spiral and axial components are frequently well-developed, often to a much greater degree than in most later nassariid species; (4) the range of body size, from more than 100 mm (undescribed form from Mississippi) to around 20 mm [*B.* "*globosus*" (Gabb, 1876)] among species of *Buccinopsis* is perhaps the most striking character of the genus; (5) protoconchs apparently are not known for any member of this genus; (6) the diversity within the genus was apparently high; seven species have been formally described, and at least that many undescribed forms are known; (7) further systematic work at the species level and above is clearly needed to clarify relationships within this group and between it and other early bucciniform taxa.

PALEOGENE OF THE GULF COASTAL PLAIN

The highly fossiliferous Lower Tertiary sediments of the Gulf coastal plain of the U. S. (Text-fig. 18) contain a large number of taxa that have, at various times, been allied with the *Bullia* group. These forms are known from Texas, Arkansas, Louisiana, Alabama, Mississippi, Georgia, and South Carolina, from sediments of Paleocene and Eocene age. Of all these taxa, only one appears to be truly related to the *Bullia* group.

Genus **BULLIA** Gray *in* Griffith and Pidgeon, 1834

Subgenus **BULLIOPSIS** Conrad, 1862a

Bullia (Bulliopsis) choctavensis (Aldrich)

Plate 7, figures 13–17; Plate 8, figures 5, 6

Melanopsis Choctavensis Aldrich, 1886, p. 35, pl. 3, fig. 8.
Nassa calli Aldrich, 1886, p. 27, pl. 5, fig. 5; Cossmann, 1901b, p. 202.
Pasithea Coctavensis [*sic*] (Aldrich). de Gregorio, 1890, p. 164, pl. 16, fig. 36[11].
Nasseburna calli (Aldrich). de Gregorio, 1890, p. 108, p. 7, figs. 62a, b[11].
Bulliopsis choctavensis (Aldrich). Harris, 1899a, p. 58, pl. 7, fig. 10; Brann and Kent, 1960, p. 140; Palmer and Brann, 1966, p. 546; Toulmin, 1977, p. 206, pl. 24, fig. 4.
Buccinanops calli (Aldrich). Palmer, 1937, p. 294, pl. 40, figs. 7, 9[11]; Palmer and Brann, 1966, p. 532.
Desorinassa calli (Aldrich). Cernohorsky, 1984, p. 22.

Occurrence.—Alabama, Nanafalia Formation, Hatchetigbee Formation, Lisbon Formation.

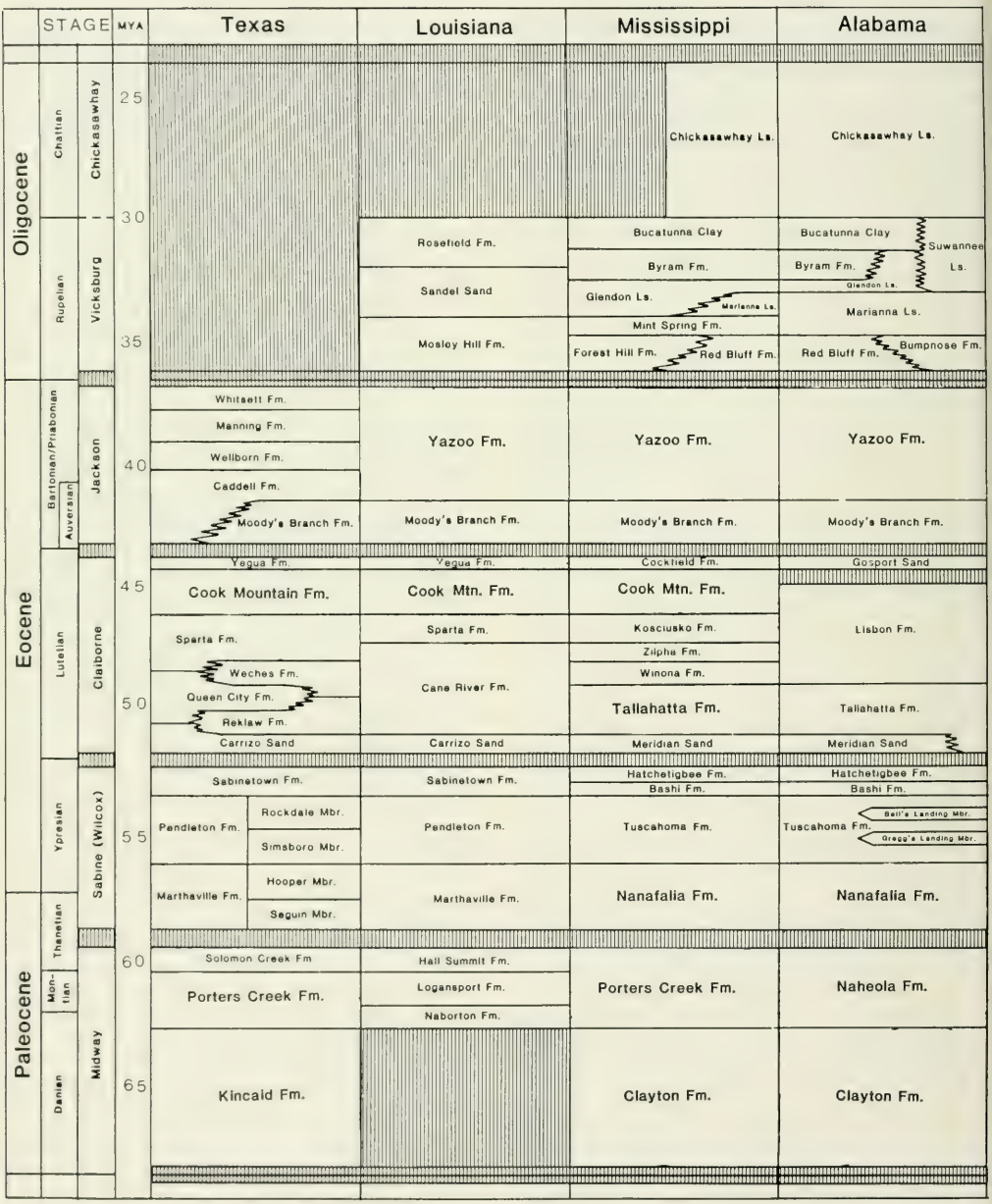
Range.—Upper Paleocene–middle Eocene.

Type locality.—Hatchetigbee Bluff, Tombigbee River, Washington County, Alabama.

Material examined.—Syntype (*M. choctavensis*), USNM 638787 (Washington County, Alabama); Topotypes MCZ(IP) 29192, USNM 434047 (Washington County, Alabama); Holotype (*N. calli*), USNM 638770 (Lisbon Bluff, Alabama River, Monroe County, Alabama); non-type material, MCZ(IP) 29250, 29251 (Dale County, Alabama) [total: 70 specimens].

Description.—Small to average size for subgenus, most specimens 10–12 mm total height, at least one exceeding 30 mm. Spire approximately one-third total height. Apex blunt, protoconch probably large and paucispiral. Aperture and body whorl relatively large. Body whorl and penultimate spire whorl usually show slight subsutural shouldering. Body whorl profile straight-sided to slightly convex. Shell surface smooth and usually shiny, external sculpture consisting of spiral ridges and grooves around anterior neck and on posterior end of whorl just below suture, forming a subsutural collar or band. Faint axial ribs often present on posterior end of early teleoconch whorls. Parietal callus well-developed, smooth-margined on body

[11] copies Aldrich, 1886, pl. 3, fig. 8.



Text-figure 18—Generalized correlation chart for the Paleogene sediments of the Gulf coastal plain. Facies relationships are schematic (simplified from Carter, 1984, unpublished, and other sources).

whorl. Anterior canal relatively short. Terminal columellar fold distinct. Posterior edge of fasciole marked by slight ridge that in larger specimens may form boundary of a shallow recurved channel around the dorsal side of neck.

Remarks.—When originally described, these gastropods were placed in two different genera in two different orders. Yet Aldrich's 1886 descriptions of *Melanopsis choctavensis* and *Nassa calli* alone suggest that these two taxa differ little in any feature other than size, a point made later by Harris (1899a, p. 58) who considered them synonymous and placed them in *Bulliopsis*. Reexamination of these forms supports Harris on both points; these shells can be placed in a single, somewhat variable species, and this species shows sufficient similarities to the middle Atlantic Miocene species treated in the preceding section to be included with them in the genus *Bullia*, subgenus *Bulliopsis*.

The holotype (and apparently only known specimen) of *Nassa calli* Aldrich, 1886 measures approximately 30 mm total height (Pl. 7, figs. 13a, b). In contrast, of the many specimens of *Melanopsis choctavensis* Aldrich, 1886 known from its type locality at Hatchetigbee Bluff, only a single known specimen (USNM 434947) exceeds 12 mm total height, measuring approximately 16 mm. This distribution of sizes in time and space is difficult to understand. It seems unlikely that only juveniles would be known from the Hatchetigbee Bluff locality. It is possible that the small average size of specimens from this locality is a result of environmental conditions, which were probably those of a relatively quiet, shallow, restricted bay (Ward, oral commun., 1987). These conditions may have placed unusual morphological demands or had peculiar ecophenotypic effects on other gastropod taxa, for example leading to the development of expanded parietal calluses (Allmon, unpublished data).

Alternatively, the type of *N. calli* could be the odd occurrence requiring explanation. This unique specimen is two to three times the size of any other known specimen, and shows some morphological differences from the Hatchetigbee specimens. The anterior end of the columella and fasciole are more inflated and pointed than in the smaller, earlier specimens. More conspicuously, the *calli* holotype shows development of a shallow recurved siphonal channel around the dorsal side of the fasciole. Although this feature suggests similarity with *Dorsanum miran* (Bruguière, 1789) and other fossil forms discussed in later sections, this likeness appears to be superficial. A moderately developed ridge bounding the posterior edge of the fasciole is present in even small specimens of *choctavensis* from Hatchetigbee Bluff, becoming more prominent in larger specimens. In the very large *calli* type specimen, a parallel anterior ridge is also developed, and a channel is formed. This channel is not so profound, however, and distinct a feature as that shown by *D. miran* and for example by some forms of "*Molopophorus*" from the Tertiary of California (see p. 65). Well-developed recurved siphonal channels are present in individuals of all sizes in these forms, rather than in only the largest. Aside from these size and fasciolar differences, furthermore, these Alabama specimens are all virtually identical in shape, proportions, and external sculpture. The *calli* type specimen may be pathological, or itself may have been subject to unusual ecophenotypic effects. Its uniqueness in size and stratigraphic position seem to support such an interpretation. The presence of a moderate siphonal channel in this single specimen thus would seem to be an individual variant, without phylogenetic significance.

The morphological similarity of these specimens suggests that only a single species should be recognized. By the "Principle of the First Reviser" (ICZN, 1985, Art. 24, p. 53), Harris' (1899a) choice of *choctavensis* in his synonymy gives this name precedence.

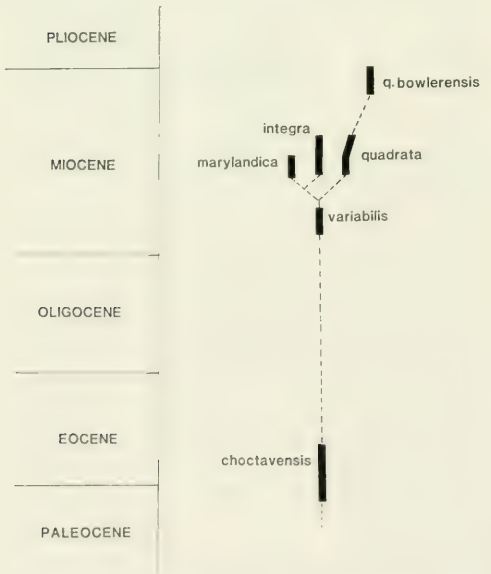
The Alabama forms resemble Mid-Atlantic Miocene *Bulliopsis* in the general ovate form of the shell, including the proportions of the spire and aperture, and also in the form of the callus, fasciole, and anterior end of the columella. It is significant that *choctavensis* especially resembles *Bulliopsis variabilis* (Whitfield, 1894), differing primarily in the presence of spiral lines or lirae on the abapical and adapical margins of its whorls.

These Alabama forms are very similar to species of *Desorinassa* Nuttall and Cooper, 1973 from western Europe, especially *D. desori* (Deshayes, 1865) [see Pl. 15, figs. 4, 5]. They are similar in details of the apex, spiral sculpture, overall form, and aperture shape. They differ, however, in the following features: (1) *D. desori* lacks a well-developed parietal callus on the inner lip of the aperture, but is otherwise very similar to *choctavensis* and *calli*. *D. lata* (Deshayes, 1865), on the other hand, shows a moderate callus but lacks many of the similarities in sculpture and proportion; (2) species of *Desorinassa* have slightly but distinctly shouldered whorls. Shouldering is variable in *choctavensis*; the *calli* type specimen shows very little; (3) the growth lines in *Desorinassa* are more pronounced than those of the Alabama forms; (4) the anterior end of the columella differs slightly; in the Alabama species it is more expanded, with the terminal fold oriented more towards the aperture and the anterior fasciolar ridge more pronounced than in *Desorinassa*. While recognizing a great degree of similarity (and phylogenetic relationship — see p. 108) between the European Paleocene forms and these two Alabama Eocene species,

it is, therefore, preferable for the time being to keep them in separate genera.

Bulliopsis choctavensis s. s. has previously been reported only from the upper lower Eocene Hatchetigbee Formation of southwestern Alabama (Toulmin, 1977, p. 206). Well-preserved specimens agreeing with *B. choctavensis* also occur, however, in the Nanafalia Formation exposed in Dale County in southeastern Alabama (Toulmin, 1977, locality ADa-2) [see Pl. 7, figs. 17a, b]. The Nanafalia and the overlying Tuscahoma Formation have long been considered to be of early Eocene age. However, recent micropaleontological work has suggested that both of these formations are of late Paleocene age (Oliver and Mancini, 1980; Gibson, Mancini, and Bybell, 1982; Frederiksen, Gibson, and Bybell, 1982). The Nanafalia occurrence extends the stratigraphic range of *B. choctavensis*, although its geographic range still appears limited. Nanafalia specimens show somewhat more spiral sculpture on the body whorl and have slightly wider apertures. They range from approximately 8 to 15 mm total height, making them intermediate between the average for Hatchetigbee specimens and the *calli* holotype. Maximum size thus may have fluctuated during the history of this lineage, and did not show the unidirectional increase that would be apparent if only the Hatchetigbee and Lisbon specimens were known.

Text-figure 19 is a phylogenetic tree diagram depicting possible relationships between the seven taxa of *Bulliopsis* discussed in this paper.



Text-figure 19.—Summary phylogenetic tree for all species of *Bullia* (*Bulliopsis*). Solid lines represent known stratigraphic ranges of species and subspecies; dashed lines represent inferred phylogenetic relationships.

Problematic Taxa allied to *Bullia*

Other taxa from the Gulf coast Paleogene that have previously been allied with *Bullia* have yet to be studied in sufficient detail to allow a complete revision and hypothesis of their relationships to be presented here. It is clear, however, that most of these taxa do not belong within the *Bullia* group as defined here, and probably do not belong to the family Nassariidae. In most cases their correct familial position is, for the present at least, obscure. They are summarized here under their most common or recent generic placement.

Incertae Sedis

Subgenus **BULLIA** Gray *in* Griffith and Pidgeon, 1834

"**Bullia**" **altilis** (Conrad)
Plate 9, figure 10

Ancillaria altile Conrad, 1832b, p. 24, pl. 10, fig. 2 [reprint, 1893, p. 42, pl. 10, fig. 2].
Ancillaria subglobosa Conrad, 1832b, p. 25, pl. 10, fig. 3; Lea, 1849, p. 96; Harris, 1895b, p. 43.
cf. *Ancillaria subglobosa* Conrad. Aldrich, 1886, pp. 50, 51, 58.
Anolax gigantea Lea, 1833, p. 180, pl. 6, fig. 193.
Ancyllaria subglobosa (Conrad). d'Orbigny, 1850, p. 352.
Ancilla altilis (Conrad). Conrad, 1854, p. 30; de Gregorio, 1890, p. 55, pl. 3, figs. 21, 22, 57, 62, 67.
Ancilla subglobosa (Conrad). Conrad, 1854, p. 30; de Gregorio, 1890, p. 56, pl. 4, figs. 3, 4, 19, 20.
Tritia altilis (Conrad). Conrad, 1862b, p. 562.
Ancillopsis subglobosa (Conrad). Conrad, 1865a, p. 22; Conrad, 1866a, p. 17; Gardner, 1945, pp. 199–200, pl. 22, figs. 20, 21.
Ptychosalpinx altilis (Conrad). Gill, 1867, p. 154.
Expleritoma prima Aldrich, 1886, p. 29, pl. 5, fig. 1; de Gregorio, 1890, p. 108, pl. 8, fig. 26, 27.
Buccinanops altile (Conrad). Cossmann, 1893, p. 33; Cossmann, 1899, p. 45.
cf. ? *Buccinanops altile* (Conrad). Veatch and Stephenson, 1911, p. 295
Buccinanops subglobosum (Conrad). Cossmann, 1893, p. 33.
Buccinanops (*Brachysphingus*) *subglobosa* (Conrad). Cossmann, 1901b, p. 221, pl. 9, fig. 14[12].
Bullia altile harrisi Palmer *in* Price and Palmer, 1928, p. 29, pl. 7, figs. 7, 11, 12, 15.
Bullia altile Conrad. Palmer *in* Price and Palmer, 1928, p. 28, pl. 6, figs. 13, 14, 16
Bullia altilis (Conrad). Palmer, 1937, p. 287, pl. 39. figs. 7–9; Dockery, 1977, pp. 73–74, pl. 14, figs. 8, 9; Toulmin, 1977, pp. 276–277, pl. 45, fig. 9.
Bullia altile (*B. subglobosum* form) (Conrad). Palmer *in* Price and Palmer, 1928, p. 29, pl. 7, figs. 13, 14, 16.

[12] the captions for figures 14 and 23 are reversed.

Bullia altilis subglobosa (Conrad). Palmer, 1937, p. 289, pl. 39, figs. 1, 4, 5, 6, 11, 12; pl. 40, figs. 1–3, 5; Palmer and Brann, 1966, p. 543.
Bullia altilis harrisi Palmer. Palmer, 1937, p. 290, pl. 39, figs. 2, 3, 10, 13; Brann and Kent, 1960, p. 139; Palmer and Brann, 1966, p. 543.
Ancillopsis harrisi (Palmer). Gardner, 1945, p. 200, pl. 22, figs. 22, 23.
cf. *Bullia altilis* (Conrad). Harris and Palmer, 1947, p. 347, pl. 45, figs. 22, 23.
cf. *Bullia altilis subglobosa* (Conrad). Harris and Palmer, 1947, p. 348, pl. 45, fig. 24; Brann and Kent, 1960, p. 139.
Bulla [*sic*] *altilis subglobosa* (Conrad). Wilbert, 1953, p. 99.
? *Bullia calluspira* Dockery, 1980, pp. 109–110, pl. 3, figs. 4–7.

Occurrence.—Alabama, Bashi Formation, Gosport Sand, Lisbon Formation, Nanafalia Formation; Mississippi, Moody's Branch Formation; Arkansas, White Bluff Formation; South Carolina (?), McBean Formation; Georgia, Barnwell Sand (?); Texas, Queen City Formation; Tamaulipas, Mexico, Jackson Formation, Laredo Formation.

Range.—Lower–upper Eocene.

Type locality.—[for *A. altile* Conrad, 1832b] Claiborne Bluff, Alabama River, Monroe County, Alabama.

Material examined.—Lectotype (plus eight specimens) of *A. altile* (selected by Palmer, 1937, p. 289 [*fide* Moore, 1962, p. 36]), ANSP 14644 (Monroe County, Alabama); Holotype of *B. altilis harrisi*, PRI 360; Paratypes, PRI 356, 357 (all from Bastrop County, Texas); Lectotype (plus seven specimens) of *B. altilis subglobosa* (selected by Palmer, 1937, p. 290 [*fide* Moore, 1962, p. 99]), ANSP 14645 (Monroe County, Alabama); Holotype of *Expleritoma prima*, USNM 638776 (Salitpa Creek, Alabama); Holotype of *B. calluspira*, PRI 30022 (Lauderdale County, Mississippi); Hypotypes, USNM 497245 (Tamaulipas, Mexico), 497255 (Nuevo Leon, Mexico); non-type material: MCZ(IP) 29242 (Clarke County, Alabama), 29243 (Washington County, Alabama), 29244 (Lauderdale County, Mississippi), 29245 (Clarke County, Alabama) [total: 59 specimens].

Remarks.—Pending a detailed revision of these forms, it is not possible to say exactly how many species exist within what may be informally referred to as the "*Bullia*" *altilis* complex. Individuals assignable to this group have a very inflated body whorl that is usually dorsoventrally compressed, often to the point of being quite flat in overall form. The parietal callus is always expanded, sometimes enormously so, and covers much of the ventral surface of the shell. There is usually little or no visible external sculpture aside from weakly marked growth lines. The anterior siphonal notch is moderately developed, but the fasciole is weak or absent. The anterior end of the columella is usually simple and pointed and there does not seem to be a terminal fold in well-preserved specimens.

Conrad described the species *Ancillaria altile* and *A. subglobosa* from the same deposits, at Claiborne Bluff on the Alabama River, and the two taxa were generally treated as distinct species until Palmer (1937, p. 283) suggested that "*B. subglobosa* appears to be only a variety of the more normal form, *altilis*." It has generally been held that the two forms can be distinguished by the relative height of the spire in adult specimens; in *altilis* s. s., the spire is usually higher (though never greater than one-third total height), giving the posterior end of the shell an attenuated appearance, in contrast to the gross inflation of the body whorl. In *subglobosa*, the spire ranges from being a small point on the posterior of the shell to being virtually absent. Palmer also stated, however, that "immature specimens do not show characters distinctive of either form. The young shells have the apex of the spire acute."

As these two forms occur in the same horizons and localities, they cannot be designated as distinct subspecies. Examination of larger samples will be necessary to determine if the high- and low-spired forms grade into one another at these localities, or whether the ontogenetic features noted by Palmer will actually allow reseparation of the two as distinct species.

Palmer (*in* Price and Palmer, 1928) described another subspecies, *B. altilis harrisi*, from lower Claiborne sediments of Bastrop County, Texas. As this form appears to be morphologically distinct and geographically separated from *altilis* s. s. from farther east, designating it as a distinct subspecies may be justifiable.

Gardner (1945, pp. 199–200) described specimens she claimed were referable to these taxa [she used the names *Ancillopsis subglobosa* (Conrad, 1832b) and *A. harrisi* (Palmer *in* Price and Palmer, 1928) from the middle and upper Eocene of northeastern Mexico and southern Texas, noting extreme development of the callus over most of the shell in many specimens.

Dockery (1980) has described *Bullia calluspira*, which is clearly closely related to this complex (see Pl. 9, fig. 11). *B. calluspira* most closely resembles some individuals of *B. altilis subglobosa* (Conrad, 1832b), especially in its much expanded callus. There do not appear to be intergradations between these forms, however, and they do not appear to co-occur stratigraphically (Dockery, written commun., 1986). *B. calluspira* may thus represent a distinct taxon.

Cossmann (1893) was the first to unite these forms with the *Bullia* group, placing *altile* in the genus *Buccinanops*, subgenus *Brachysphingus*. Palmer (1937) moved the species to the genus *Bullia*, but did not detail the morphologic basis for this decision, except to note that some specimens of *B. altilis harrisi* Palmer

in Price and Palmer, 1928 "show the anterior notch and groove of *Bullia*" (Palmer, 1937, p. 290). Based on examination of the type specimens, my own collections, and of all published figures and descriptions, I fail to see any character or aspect of overall form which might be considered as compelling evidence for including these forms in the genus *Bullia* as discussed in this paper. I tentatively suggest that the "*Bullia*" *altilis* complex belongs to an undescribed genus, probably not within Nassariidae. Cernohorsky (1984, p. 26) has suggested that "*Expleritoma prima*" Aldrich, 1886 [= *Bullia altilis*] "resembles a naticoid far more closely than any genus of Nassariidae." Recent and fossil species of *Amalda* Adams, 1853 (Olividae, Ancillinae) from the Indo-West Pacific illustrated by Michaux (1989) are extraordinarily similar to these Gulf Coast species, and may belong to the same group.

Other taxa probably closely related to this complex are "*Bullia*" *tuomeyi* (Aldrich, 1921) and "*Buccinanops*" *ellipticum* (Whitfield, 1865) from the Eocene of Alabama (see p. 59) and "*Buccinanops*" *patulum* Deshayes, 1835 from the Eocene of the Paris Basin (see p. 86).

"**Bullia**" **scamba** (Conrad)
Plate 9, figure 2

Ancillaria scamba Conrad, 1832b, p. 25, pl. 10, fig. 4 [reprint, 1893, p. 43, pl. 10, fig. 4].
? *Anolax plicata* Lea, 1833, p. 181, pl. 6, fig. 194; Lea, 1849, p. 96; Harris, 1895b, p. 35.
Ancilla scamba (Conrad). Conrad, 1854, p. 30; de Gregorio, 1890, p. 55, pl. 4, figs. 12, 13, 15, 16[13].
Ancillopsis scamba (Conrad). Conrad, 1865a, p. 22; Conrad, 1866a, p. 17.
Olivula ? *plicata* (I. Lea). Conrad, 1865a, p. 22; Conrad, 1866a, p. 17.
Ancillaria (*Ancillopsis*) *scamba* Conrad. Tryon, 1883, p. 61, pl. 3, fig. 26.
Ancilla (*Olivula*) *plicata* (I. Lea). de Gregorio, 1890, p. 57, pl. 4, fig. 9[14]; Cossmann, 1901b, p. 223.
Ancillina scamba (Conrad). Cossmann, 1893, p. 40.
Ancillina ? *plicata* (I. Lea). Cossmann, 1893, p. 40.
Buccinanops (*Bullia*) *scambum* (Conrad). Cossmann, 1901b, p. 223, pl. 9, fig. 23[15].
Bullia scamba (Conrad). Palmer, 1937, p. 290, pl. 44, figs. 2, 7; Brann and Kent, 1960, p. 140; Glibert, 1963, p. 98; Palmer and Brann, 1966, p. 544.

Occurrence.—Alabama, Gosport Sand.

Range.—Middle Eocene.

Type locality.—Claiborne Bluff, Alabama River, Monroe County, Alabama.

Material examined.—Lectotype (plus ten specimens) (selected by Palmer, 1937, p. 291 [*fide* Moore, 1962, p. 95]), ANSP 14647 (Monroe County, Alabama); Hypotype, PRI 3082 (Monroe County, Alabama) [total: 12 specimens].

Remarks.—Available specimens of this form are all badly worn, and details are difficult to discern. They seem to resemble most closely "*Bullia*" *tenera* (Conrad, 1834). Both species have relatively large body whorls, large apertures, and small apical angles, and both show a single prominent ridge bordering the fasciole. At least some specimens of *scamba* show faint axial ribbing on early teleoconch whorls. Later whorls are devoid of sculpture in both *tenera* and *scamba*. Palmer (1937, p. 291) suggested that *Anolax plicata* Lea, 1833 [the lectotype of which, ANSP 5910, is apparently lost] may actually have been a juvenile of "*Bullia*" *tenera* rather than "*B.*" *scamba*.

"**Bullia**" **tenera** (Conrad)
Plate 9, figures 1, 3

Ancillaria tenera Conrad, 1834, p. 147; Conrad, 1835, p. 42, pl. 16, fig. 5 [reprint, 1893, p. 98, pl. 16, fig. 5].
Ancilla tenera (Conrad). Conrad, 1854, p. 30; de Gregorio, 1890, p. 56, pl. 4, fig. 2[16].
Ancillopsis tenera (Conrad). Conrad, 1865a, p. 22; Conrad, 1866a, p. 17.
Bullia tenera (Conrad). Palmer, 1937, p. 291, pl. 42, figs. 7–13; Brann and Kent, 1960, p. 140; Palmer and Brann, 1966, p. 54.

Occurrence.—Alabama, Gosport Sand; Louisiana, Texas, Cook Mountain Formation.

Range.—Middle Eocene.

Type locality.—Claiborne Bluff, Alabama River, Monroe County, Alabama.

Material examined.—Holotype, ANSP 14646 (Monroe County, Alabama); Hypotypes, PRI 3065, (Louisiana), 3066 (Burleson County, Texas), 3074 (Louisiana).

Remarks.—As noted by Palmer, there appears to be considerable variation in form among individuals of this species. Relative spire height, degree of shouldering of the whorls, and degree of flare of the aperture all vary with ontogenetic stage and among individuals of similar size. There is frequently incipient to pronounced axial sculpture on the whorl shoulders, but preservation is usually too poor to discern details of this feature. The shape of the body whorl is also variable, with a weak to pronounced oblique spiral ridge present on or absent from the middle of the whorl. If a ridge is present, the anterior half of the body whorl may appear to be bent toward the aperture, and the margin of the body whorl is distinctly angled. If it is absent, the margin of the body whorl is smoothly curved from the suture to the anterior canal. The anterior end of the columella is relatively simple, but there is usually a pronounced oblique spiral ridge bounding the fasciole. The columella lacks a terminal fold.

[13] copies Conrad, 1832b, pl. 10, fig. 4.

[14] copies Lea, 1833, pl. 6, fig. 194.

[15] the plate captions for figures 23 and 14 are reversed.

[16] copies Conrad, 1835, pl. 16, fig. 5.

"*Bullia*" *tenera* differs from "*B.*" *scamba* (Conrad, 1832b) mainly in having a proportionately lower spire and larger aperture. Both forms are reported by Palmer from the Gosport Sand at Claiborne, Alabama. Considering the wide range of variation shown by specimens assigned to *tenera*, it is possible that further study will show the two forms to be conspecific. In any case, neither shows any trace of a terminal columellar fold and they do not otherwise resemble other species of the *Bullia* group. I conclude that they are probably not related to this group.

"Bullia" tuomeyi (Aldrich)
Plate 9, figure 13

Ancillopsis Tuomoyi [*sic*] Aldrich, 1921, p. 12, pl. 1, figs. 23, 24.
Bullia tuomeyi (Aldrich). Palmer and Brann, 1966, p. 545.

Occurrence.—Alabama, Greggs's Landing and Bell's Landing members, Tuscahoma Formation.

Range.—Upper Paleocene.

Type locality.—Bell's Landing, Alabama River, Monroe County, Alabama.

Material examined.—Holotype, GSATC 39 (Monroe County, Alabama).

Remarks.—Aldrich's original description is unusually complete and accurate. This form resembles members of the "*Bullia*" *altilis* complex in its very low spire, large flattened body whorl, simple columella, and enlarged callus, but differs in its possession of a channeled sutural groove above the body whorl, and its differential inflation of the posterior end of the shell rather than the middle, leading the anterior end to show a tapered, flattened appearance. It is almost certainly closely related to this complex, and not related to the *Bullia* group.

Subgenus **ANBULLINA** Palmer, 1937

Type species.—(by original designation) *Ancillaria ancillops* Heilprin, 1891.

"Bullia (Anbullina)" ancillops (Heilprin)
Plate 9, figure 4

Ancillaria ancillops Heilprin, 1891, pp. 398, 406, pl. 11, fig. 4.
Buccinanops (*Bullia*) *ancillopsis* [*sic*] (Heilprin)[17]. Cossmann, 1901b, p. 223, pl. 9, fig. 24
Bullia (*Anbullina*) *ancillops* (Heilprin). Palmer, 1937, p. 292, pl. 40, figs. 4, 6; Wenz, 1943, p. 1226, fig. 3488[18].
Bullia cf. *B.* (*Anbullina*) *ancillops* (Heilprin)[19]. Dockery, 1980, p. 110, pl. 17, fig. 4.

Occurrence.—Texas, Weches Formation; Mississippi, Doby's Bluff Tongue of Kosciusko Formation (?).

Range.—Lower–middle Eocene.

Type locality.—Smithville, Bastrop County, Texas.

Types.—Holotype lost [*fide* Palmer, 1937, p. 293].

Material examined.—Hypotype, PRI 3045 (Bastrop County, Texas).

Remarks.—This species was first allied with the *Bullia* group by Cossmann (1901b), who placed it in the genus *Buccinanops*, subgenus *Bullia*. Palmer (1937) proposed *Anbullina* as a subgenus within *Bullia*, with this species as its only representative. Palmer stated that *ancillops* differed from *Bullia* s. s. "in the character of the band below the suture, the presence of the plications on the apical whorls and the groove in the umbilical area," but she did not explicitly describe its resemblances to *Bullia* s. s., which seem to consist of little more than overall similarity of shape. The Alabama species is, furthermore, much more low-spired than almost all living species of the *Bullia* group. It shows no trace of a terminal columellar fold and, as mentioned by Palmer, has a unique columellar form she described as a "false umbilicus". I cannot see any reason for allying this species with the *Bullia* group or Nassariidae, and its position is uncertain. According to Palmer (1937) and Palmer and Brann (1966), it is known only from Smithville, Bastrop County, Texas, a classic locality that is now inaccessible.

Genus **BUCCINANOPS** d'Orbigny, 1841

"Buccinanops" ellipticum (Whitfield)
Plate 9, figure 8

Pseudoliva elliptica Whitfield, 1865, p. 260; Aldrich, 1886, p. 56; Aldrich, 1887[20], p. 80; Gardner, 1945, p. 195, pl. 27, figs. 3, 4.
Buccinanops ellipticum (Whitfield). Harris, 1899a, p. 30, pl. 3, figs. 14, 15; Harris, 1899b, p. 305, pl. 54, figs. 4, 5; LeBlanc, 1942, p. 117, pl. 15, figs. 1, 2; Brann and Kent, 1960, p. 134; Palmer and Brann, 1966, p. 533.

Occurrence.—Alabama, Bell's Landing Member, Tuscahoma Formation; Texas, Pendleton Formation; Mississippi, Moody's Branch Formation.

Range.—Upper Paleocene–upper Eocene.

Type locality.—Probably Bell's Landing, Alabama River, Monroe County, Alabama (not "Vicksburg" as stated by Whitfield [*fide* Aldrich, 1887, p. 80]).

Material examined.—Holotype, FMNH-UC 24670; Hypotype, LSU 6023 (Pendleton Bluff, Sabine River, Sabine County, Texas); non-type material, MCZ(IP) 29241 (Clarke County, Mississippi) [total: five specimens].

Remarks.—This form most closely resembles taxa of the "*Bullia*" *altilis* complex. It is lanceolate to elliptical in shape, with an evenly curved profile attenuated at both apical and anterior ends. The spire is relatively low, comprising not more than one-fourth

[17] not *Anaulax ancillopsis* Heilprin as by Cossmann (p. 223).
[18] copies Palmer, 1937, pl. 40, fig. 6.
[19] misspelled on plate as *Bucilla* cf. (*Anbullina*) *ancillops*.
[20] not "1897" as in Harris (1899a) and LeBlanc (1942).

the total height, while the aperture comprises more than one-half. Sculpture is lacking, other than growth lines. The columella bears no trace of a terminal fold. A potentially important feature may be a variable band (similar in orientation to that in *Bulovia weisbordi* Palmer, 1937) running across the dorsal surface of the shell and around, from outer lip of the aperture to the parietal callus. In the type specimen, this band takes the form of an adapertural angular deflection of the growth lines, forming shallow chevrons. On specimens from the Moody's Branch Formation of Mississippi, there is a single shallow groove approximately 1–2 mm wide (see further discussion under *Monoptygma curtum* on p. 61).

Genus **BULOVIA** Palmer, 1937

Type species.—(by original designation) *Bulovia weisbordi* Palmer, 1937.

Bulovia weisbordi Palmer
Plate 9, figure 5

Bulovia weisbordi Palmer, 1937, p. 293, pl. 40, figs. 10, 11; Wenz, 1943, p. 1226, fig. 3489[21]; Brann and Kent, 1960, p. 140.
Bullia (Bulovia) weisbordi (Palmer). Cernohorsky, 1982, p. 17-240.

Occurrence.—Texas, Weches Formation.
Range.—Middle Eocene.
Type locality.—Smithville, Bastrop County, Texas.
Material examined.—Holotype, PRI 3048.
Remarks.—This species is apparently known only from the holotype specimen. It resembles so closely specimens described by Palmer (1937) as belonging to the oliviid *Agaronia alabamiensis* (Conrad, 1833b) that on first inspection it is very difficult to separate the two. The fasciole of *B. weisbordi* forms a single elongate fold oriented parallel to the aperture, and bounded on the whorl side by a deep depression. The most distinctive feature is a pair of parallel grooves extending from the anteriormost point of the outer apertural lip dorsally around the body whorl to the callus. *A. alabamiensis* shows only a single such groove, and its fasciole is recognizably different. Both species have grooved sutures, more pronounced in *B. weisbordi* than *alabamiensis*. *Bulovia weisbordi* does not show any terminal columellar fold and is not a nassariid. I suggest that it may be most closely related to oliviids such as *Agaronia*. *A. alabamiensis* is one of the most abundant forms in the Gosport Sand, and also occurs in the lower Claiborne Group. *B. weisbordi* is known only from the now inaccessible Smithville outcrop of the Weches Formation of Texas.

[21] copies Palmer, 1937, pl. 40, fig. 10.

Genus **MONOPTYGMA** Lea, 1833

Type species.—(by subsequent designation [Cossmann, 1899] *Monoptygma lymneoides* (Conrad, 1833b).

Monoptygma lymneoides (Conrad)

Ancillaria lymneoides Conrad, 1833b, p. 44; Conrad, 1834, p. 5; Conrad, 1835, p. 42, pl. 16, fig. 6; Lea, 1849, p. 96; Harris, 1895b, p. 26.
Monoptygma alabamiensis Lea, 1833, p. 186, pl. 6, fig. 201; Lea, 1849, p. 102; Conrad, 1865a, p. 22; Conrad, 1866a, p. 17; Harris, 1895b, p. 3.
Ancyllaria [*sic*] *lymneoides* Conrad. d'Orbigny, 1850, p. 352.
Ancilla lymneoides (Conrad). Conrad, 1854, p. 30.
Monoptygma lymneoides (Conrad). Conrad, 1865a, p. 23; Conrad, 1866a, p. 17; Tryon, 1883, pp. 61, 91, pl. 3, fig. 23; Wenz, 1943, p. 1227–1228, fig. 3492[22]; Brann and Kent, 1960, p. 567; Glibert, 1963, p. 99; Palmer and Brann, 1966, pp. 779–780.
Ancilla (Monoptygma) Alabamiensis (I. Lea). de Gregorio, 1890, p. 58, pl. 4, fig. 10[23].
Ancilla (Monoptygma) lymneoides (Conrad). de Gregorio, 1890, p. 58, pl. 4, fig. 14[24].
Monoptygma limneoides [*sic*] (Conrad). Cossmann, 1893, p. 41; Cossmann, 1899, p. 71, pl. 3, figs. 24, 25.
Monoptygma lymneoidies [*sic*] (Conrad). Palmer, 1937, p. 296–297, pl. 38, figs. 19, 20, pl. 85, figs. 3, 7.

Occurrence.—Alabama, Gosport Formation.
Range.—Middle Eocene.
Type locality.—Claiborne Bluff, Alabama River, Monroe County, Alabama.
Material examined.—Hypotype, PRI 3036 (Monroe County, Alabama); non-type material, MCZ(IP) 29252 (Monroe County, Alabama) [total: two specimens].
Other types.—Lectotype (selected by Palmer, 1937, p. 297), ANSP 15619; Holotype of *M. alabamiensis* Lea, ANSP 5929.
Remarks.—(see below, under *Monoptygma curtum*).

Monoptygma leai Whitfield
Plate 9, figure 9

Monoptygma leai Whitfield, 1865, p. 261, pl. 27, fig. 7; Aldrich, 1887, p. 80; Palmer, 1937, p. 297, pl. 38, figs. 1, 2, 6, 8; Gardner, 1945, p. 195, pl. 27, figs. 2, 5; Brann and Kent, 1960, p. 567; Palmer and Brann, 1966, p. 779.

Occurrence.—Alabama, Lisbon Formation.
Range.—Middle Eocene.
Type locality.—Lisbon Bluff, Alabama River, Monroe County, Alabama (*fide* Aldrich, 1887).
Material examined.—Syntypes, FMNH-UC 24671 [five specimens] (Monroe County, Alabama); Hypotype, PRI 3026 (Monroe County, Alabama).
Remarks.—(see below, under *Monoptygma curtum*).

[22] copies Palmer, 1937, pl. 38, fig. 19.
[23] copies Lea, 1833, pl. 6, fig. 201.
[24] copies Conrad, 1835, pl. 16, fig. 6.

Monoptygma crassiplicum Conrad

Monoptygma crassiplica Conrad *in* Gabb, 1860, p. 384, pl. 67, fig. 37; Conrad, 1865a, p. 22; Conrad, 1866a, p. 17; Palmer, 1937, p. 298, pl. 38, figs. 3–5; Brann and Kent, 1960, p. 567.
Monoptygma crassiplicum Conrad. Palmer and Brann, 1966, pp. 778–779.

Occurrence.—Texas, Weches Formation; Louisiana, Cook Mountain Formation.

Range.—Middle Eocene.

Type locality.—Near Wheelock, Robertson County, Texas.

Type.—Holotype lost [*fide* Moore, 1962, p. 51].

Material examined.—Hypotype, PRI 3027 (Ouachita Parish, Louisiana).

Remarks.—(see below, under *Monoptygma curtum*).

Monoptygma curtum Conrad

Monoptygma curta Conrad, 1865a, p. 22; Conrad, 1865c, p. 143, pl. 11, fig. 8; Conrad, 1866a, p. 17; Harris, 1895b, p. 14; Cossmann, 1899, p. 72; Palmer, 1937, p. 298, pl. 85, fig. 8.
Ancilla (*Monoptygma*) *curta* (Conrad). de Gregorio, 1890, p. 58, pl. 4, fig. 11[25].
Monoptygma curtum Conrad. Palmer and Brann, 1966, p. 779.

Occurrence.—Alabama, Gosport Sand.

Range.—Middle Eocene.

Type locality.—Claiborne Bluff, Alabama River, Monroe County, Alabama.

Material examined.—Holotype, ANSP 15618.

Remarks.—This species is apparently known only from the type specimen (Palmer, 1937, p. 298). Palmer (1937) moved the genus *Monoptygma* Lea from Olividae, to which it had been referred by most previous workers, to Nassariidae, in which, she said, its affinities "seem to be with *Bullia*" (Palmer, 1937, p. 296). Palmer listed four species of the genus. Although they range in total height from 1–4 cm, all share a similar lanceolate shape and large aperture, but lack a distinct terminal columellar fold, the columella ending in a tapering point. All four species, however, bear a distinct fold on the middle of the parietal lip. Together with slight axial ribbing on the adapical margins of the whorls, this appears distinctive of the group. Although the complexity of their columellae is notable, the species of *Monoptygma* share many more features with forms such as "*Bullia*" *altilis* (Conrad, 1832b) and *Anbullina ancillops* (Heilprin, 1891) than they do with species of *Bullia* s. s. or *Buccinanops*. Their simple shape and lack of a distinct terminal columellar fold justify their exclusion from the *Bullia* group.

Gardner (1945, p. 195) noted that *Monoptygma leai* Whitfield, 1865 closely resembles *Pseudoliva elliptica* Whitfield, 1865 differing mainly in the lack of a medial columellar fold on the latter (cf. Pl. 9, figs. 8, 9). *P. elliptica* does not agree especially well with most other species assigned to *Pseudoliva*, and may belong to another group. As already summarized on p. 59, Harris assigned it to "*Buccinanops*". It probably belongs to an undescribed genus.

[25] copies Conrad, 1865c, pl. 11, fig. 8.

Genus **DORSANUM** Gray, 1847

Type species.—*Buccinum politum* Lamarck, 1822.

"**Dorsanum**" **bellaliratum** (Gabb)
Plate 9, figure 7

Phos bellaliratus Gabb, 1862, p. 367.
Ragenella bellalvirata [*sic*] (Gabb). Conrad, 1865a, p. 21.
Sagenella bellalirata (Gabb). Conrad, 1865b, unnumbered page.
Sagenella bellirata (Gabb). Conrad, 1866a, p. 18.
Buccinum (*Buccitriton*) *bellaliratum* (Gabb). de Gregorio, 1890, p. 106, pl. 8, figs. 20, 21.
Dorsanum (section *Sagenella*) *bellaliratus* (Gabb). Palmer, 1937, p. 299, pl. 41, fig. 1 [holotype].
Dorsanum (*Sagenella*?) *bellaliratum* (Gabb). Wenz, 1943, p. 1224, fig. 3480[26].
Dorsanum bellaliratum (Gabb). Palmer and Brann, 1966, p. 637.

Occurrence.—Alabama, Gosport Sand.

Range.—Middle Eocene.

Type locality.—Claiborne Bluff, Alabama River, Monroe County, Alabama.

Material examined.—Holotype?, ANSP 17110.

Remarks.—The synonymy of this species is complicated by the fact that Conrad (or his printers) misspelled both the genus and species names in the original description. These errors were corrected in an unnumbered two-page list appended to volume 1 of the same journal (Conrad, 1865b). The corrected generic name, *Sagenella*, however, is a primary homonym of the Paleozoic bryozoan *Sagenella* Hall, 1851.

Conrad listed two species under *Sagenella*, *S. bellalirata* and *S. texana* [*non Phos texanus* Gabb, 1860]. *S. texana*, however, is a *nomen nudum*, as he did not give a figure or description (Palmer, 1937).

Palmer (1937, p. 299) stated that the terminal columellar fold allied the species with *Dorsanum* Gray, 1847 rather than with *Buccitriton* Conrad, 1865a, but admitted that there was "a certain indefiniteness as regards the characters of the two groups." In fact, the anterior end of the columella is damaged on the holotype specimen, and the presence of any sort of terminal columellar fold is problematic. Palmer finally concluded that species assignable to *Buccitriton* and to *Dorsanum* "differ in the character of the nucleus." This statement seems to have been based on the original description of Gabb, for Palmer noted that the protoconch of the type specimen is broken. Thus while

[26] copies Palmer, 1937, pl. 41, fig. 1.

the protoconch of *D. bellaliratum* consists of three "smooth and polished" whorls (Gabb, 1862), that of *Buccitriton* "is composed of four and a half to five and a half smooth whorls, elevated, conical, the first minute, the last very large" (Palmer, 1937, p. 304). Resolution of these character distributions, and the systematic position of this form, must await examination of further material. At present it would seem most reasonable to suggest that "*Dorsanum*" *bellaliratum*, "*D.*" *scalatum*, and the various species assigned to the genus *Buccitriton* comprise a somewhat variable but related, probably non-nassariid, group of bucciniform gastropods. Determination of the systematic relationships of these and other similar bucciniform species from elsewhere may throw considerable light on the early history of both Nassariidae and Buccinidae s. l.

"Dorsanum" scalatum (Heilprin)
Plate 9, figure 6

Buccitriton scalatum Heilprin, 1891, pp. 399, 405, pl. 11, fig. 5.
Phos (*Buccitriton*) *scalatum* (Heilprin). Cossmann, 1901b, p. 160.
Dorsanum scalatum (Heilprin). Palmer, 1937, p. 300, pl. 41, figs. 5, 10; LeBlanc, 1942, p. 123 [in part; not pl. 15, figs. 5, 6]; Brann and Kent, 1960, p. 338; Palmer and Brann, 1966, p. 638.

Occurrence.—Texas, Weches Formation, Sabinetown Formation (?).

Range.—Lower–middle Eocene.

Type locality.—Smithville, Bastrop County, Texas.

Material examined.—Hypotype (Palmer, 1937), PRI 3051.

Other types.—Holotype lost [*fide* Palmer, 1937]; LeBlanc (1942) figured a hypotype (LSU 6027), but Palmer and Brann (1966, p. 638) suggest that this specimen represents an undescribed species. This hypotype specimen is also apparently lost (Phillips, written commun., 1986).

Remarks.—Palmer stated that the protoconch of this species "consists of two and a half to three, smooth whorls, first whorl minute, others rapidly increasing, globose," again contrasting this with the form of the protoconch of *Buccitriton*. Palmer also added that the outer apertural lip ("labrum") in this species "is thickened but not crenulated," but that this character seems to be highly variable. "The species is placed in the genus [*Dorsanum*]," she said, "because of the similar aperture including the single plication on the lower columella."

Although *scalatum* and *bellaliratum* may resemble each other somewhat in form of the protoconch and aperture, they are in most other ways very different, and their congeneric placement is uncertain. The whorls of *bellaliratum* are rounded while those of *scalatum* show pronounced shoulders; axial sculpture persists onto the body whorl in *bellaliratum*, but does not proceed beyond the penultimate whorl in *scalatum*; the axial ribs in *bellaliratum* are very faint compared to those on the spire of *scalatum*. The distribution of spiral grooves on the body whorl of *scalatum* is reminiscent of the pattern in other fossil species of the *Bullia* group in that grooves are faint or obsolete in the middle. Neither *scalatum* nor *bellaliratum* shows a well-developed parietal callus.

Nuttall and Cooper (1973, p. 213) suggest that their genus *Thanetinassa* from the Paleocene of Britain (Pl. 15, fig. 10) should be compared with these two species (see discussion on p. 83). *Thanetinassa* is much closer to *bellaliratum* than to *scalatum*; *bellaliratum*, however, does not show the development of a beaded subsutural band, although this could be the result of wear on the holotype specimen.

LeBlanc (1942) noted that specimens assignable to "*D.*" *scalatum* from the "Sabinetown Unit" (upper Wilcox Group, lower Eocene) of Louisiana are only about half the size of specimens from the later Claiborne Group.

Genus **LISBONIA** Palmer, 1937

Type species (by original designation).—*Ancillaria expansa* Aldrich, 1886.

Lisbonia expansa (Aldrich)

Ancillaria expansa Aldrich, 1886, p. 28, pl. 5, fig. 11.
Ancilla expansa (Aldrich). de Gregorio, 1890, p. 55, pl. 4, fig. 1[27].
Lisbonia expansa (Aldrich). Palmer, 1937, p. 295, pl. 40, figs. 8, 12, 13; Brann and Kent, 1960, p. 500; Palmer and Brann, 1966, p. 740.
Bullia (*Lisbonia*) *expansa* (Aldrich). Wenz, 1943, p. 1227, fig. 3491[28].

Occurrence.—Alabama, Lisbon Formation.

Range.—Middle Eocene.

Type locality.—Lisbon Bluff, Alabama River, Monroe County, Alabama.

Material examined.—Holotype, USNM 638775; Hypotype, PRI 3047; non-type material, MCZ(IP) 29248 (Monroe County, Alabama) [total: 15 specimens].

Remarks.—This species is a large, inflated, low-spired form very similar in general shape to "*Bullia*" *altilis* (Conrad, 1832b). In erecting the genus *Lisbonia*, Palmer (1937, p. 295) pointed out this high degree of similarity in the adult forms but stated that "the whorls of the spire not including the penultimate whorl have fine, conspicuous, longitudinal ridges," which the early whorls of *altilis* lack. She suggested that the juvenile specimens most closely resembled "*Bullia* (*Anbullina*)" *ancillops* (Heilprin, 1891) in the sculpture of the

[27] copies Aldrich, 1886, pl. 5, fig. 11.
[28] copies Palmer, 1937, pl. 40, figs. 8, 13.

spire and "the subsutural demarcation in which the retral lines of growth are conspicuous." "*Lisbonia*," she concluded, "ontogenetically and phylogenetically has continued in development beyond that of *Anbullina* and developed a large, globose shell with a large columellar callus and lost the indentation along the retral indentation of the growth lines below the suture."

Wenz (1943) placed the species in the genus *Bullia*, subgenus (*Lisbonia*), but gave no explicit justification for doing so. Whether or not this species is closely related to "*Anbullina*", it is seemingly no more closely related to the *Bullia* group than is "*Bullia*" *altilis* (Conrad, 1832b), and I do not consider it reasonable to include it in the *Bullia* group.

The genus *Pseudoliva* Swainson, 1840 (Pl. 9, fig. 15) resembles both *Lisbonia* Palmer, 1937 and the "*Bullia*" *altilis* complex, and has occasionally been allied with them. Gardner (1945, p. 199), for example, suggested that *Pseudoliva* and "*Ancillopsis*" [= "*Bullia*" *altilis* (Conrad, 1832b)] "are doubtless closely related." These resemblances are superficial, however, and not indicative of a close phylogenetic relationship. Many species of *Pseudoliva* possess an umbilicus, and almost all a single, distinct spiral groove circling the lower half of the body whorl from fasciole to outer apertural lip. These characters do not appear in any known specimens of *Lisbonia*, the "*Bullia*" *altilis* complex, or the *Bullia* group. Spire height and total size are highly variable among species of *Pseudoliva*. Species of *Pseudoliva* occur widely in Tertiary sediments in the Americas and Europe (see, *e. g.*, Squires, 1989), and at least one living species is present off West Africa (Dautzenberg, 1913, p. 30; Nickles, 1950, p. 107).

Some mention may also be made here of the only American forms recently assigned to the genus *Melanopsis* Ferussac, 1807. "*Melanopsis*" *anita* (Aldrich, 1886) is apparently known only from its type specimen (USNM 638788), a small, delicate shell from the Gregg's Landing Member of the upper Paleocene Tuscahoma Formation of Alabama (Pl. 9, fig. 14). In its inflated form, involute spire, and simple anterior columella, this specimen resembles "*Bullia*" *altilis* (Conrad, 1832b), and may represent a juvenile of a form related to this complex. It bears no resemblance whatsoever to true *Melanopsis* from Europe.

Palmer and Brann (1966, p. 755) synonymized "*Melanopsis*" *planoidea* (Aldrich, 1895) with "*M.*" *anita* (Aldrich, 1886). In its higher spire, this form resembles true melanopsids more closely, but does not resemble "*M.*" *anita*. It too lacks any characters which would link it to the *Bullia* group, or indeed to any other lineage discussed here. Like "*M.*" *anita*, "*M.*" *planoidea* seems to be known only from its type (USNM 638955), from the same horizon and locality as *anita*. These two gastropods belong to neither Melanopsidae nor the *Bullia* group.

CENOZOIC OF THE WEST COAST OF NORTH AMERICA

A large group of species, many of which have at various times been allied with the *Bullia* group, occurs in Tertiary formations of California, Oregon, Washington, British Columbia, and Alaska, and perhaps Japan and China. Most have been included in the genera *Molopophorus* Gabb, 1869 and *Brachysphingus* Gabb, 1869. Species of *Molopophorus* are common and biostratigraphically important in Tertiary formations from California to Alaska (see *e.g.*, Durham, 1944; Addicott, 1976; Addicott, 1978; Marincovich, 1983; Moore, 1984).

Gabb (1869) originally erected *Molopophorus* as a subgenus of *Bullia* Gray, 1834, with *B.* (*M.*) *striata* Gabb, 1869 as the type species. The systematic relationships of the two dozen or so species currently assigned to *Molopophorus*, however, are unclear. As emphasized by Vokes (1939) and Nuttall and Cooper (1973), the entire group is in need of a thorough revision. Cossmann (1901b) tentatively synonymized *Molopophorus* with the buccinid genus *Cominella* J. E. Gray *in* M. E. Gray, 1850. Clark and Arnold (1923) and Vokes (1939) placed *Molopophorus* in the family Alectrionidae. Several Russian workers (cited in Nelson, 1978, p. 204) have placed it in Melongenidae. As already noted, Wenz (1943) placed it in Nassidae. Nuttall and Cooper (1973) have suggested that the lectotype of *Molopophorus striatus* (Gabb, 1869) is actually a juvenile specimen of *Brachysphingus* sp., and that it neither belongs to Nassariidae nor agrees in its morphology with other species usually assigned to *Molopophorus*. Nuttall and Cooper (1973) place four of these West Coast species in the nassariid genus *Colwellia* Nuttall and Cooper, 1973, and suggest that most of the others, while probably nassariid and closely related to the other European forms they describe, "need assigning to new genera." Stewart (1927, p. 389) suggested that "*Cominella*" *ovata* (Deshayes, 1835) from the Paleocene of France, figured by Cossmann and Pissaro (1904–1913; vol. 2, pl. 37, fig. 178-4), might belong to *Molopophorus*. Nuttall and Cooper (1973) assigned this species to their genus *Desorinassa*. Vokes (1939) noted that there appear to be several distinct protoconch morphologies among the California species of *Molopophorus*, and suggested that they are only doubtfully congeneric. Cernohorsky (1984, p. 26) considers the species assigned to *Molopophorus*, *Colwellia*, and *Brachysphingus* to belong to Buccinidae s. l.

Several species from the Oligocene and lower Miocene of Japan have been assigned to *Molopophorus* (see

Oyama, Mizuno, and Sakamoto, 1960; Masuda and Noda, 1976). Zhidkova (1972, p. 66, pl. 15, fig. 3) lists "*Molopophorus* cf. *anglonana*" from the Miocene of the Kuril Islands. Marincovich (1983, p. 117) states that Zhidkova's illustration "shows a very poorly preserved specimen whose generic assignment is doubtful." A form from the Upper Tertiary of China described as *Dorsanum nodocarinatum* Wang, 1982 (pp. 159–160, pl. 8, figs. 27–30), may be related to *Molopophorus* s. l.

The species accounts that follow are not intended to be a revision of this clearly heterogeneous group. Several of these species are highly variable, and it is not clear what characters are of greatest significance within the group as a whole. Careful study of larger samples in stratigraphic and geographic context will be necessary before these issues can be addressed and a detailed revision attempted. Based on examination of type specimens for most North American species, and all published descriptions and illustrations, however, I have divided the West Coast species usually assigned to *Molopophorus* Gabb, 1869 into two groups: those that appear to be related to the *Bullia* group, and those that do not (see Table 3b). The latter may be referable to undescribed nassariid genera or to other families. Species previously assigned to *Brachysphingus* Gabb, 1869 (see Table 3b) do not appear to belong to Nassariidae (Nuttall and Cooper, 1973, p. 209, pl. 8, fig. 4), and their placement is uncertain (Pl. 10, fig. 14).

Four West Coast species formerly assigned to *Molopophorus* were placed in the nassariid genus *Colwellia* by Nuttall and Cooper (1973), and seem to be related to the *Bullia* group: *M. bretzi* (Weaver, 1912), *M. tejonensis* Dickerson, 1915, *M. antiquatus* (Gabb, 1864), and *M. cretaceus* (Gabb, 1864). The following species are also here provisionally allied with the *Bullia* group: *Molopophorus anglonanus* (Anderson, 1905), *M. matthewi* Etherington, 1931, *M. gabbi* Dall, 1909, *M. dalli* Anderson and Martin, 1914, *M. newcombei* (Merriam, 1897), *M. crooki* Clark, 1938, *M. biplicatus* (Gabb, 1866), and *M. bogachielii* (Reagan, 1909). The following species do not appear to be related to the *Bullia* group, and may or may not belong in Nassariidae: *M. striatus* (Gabb, 1869), *M. californicus* Clark and Woodford, 1927, *M. stephensoni* Dickerson, 1917, *M. effingeri* Weaver, 1942, *M. lincolnensis* Weaver, 1916, *M. fishii* (Gabb, 1869), *M. aequicostatus* Vokes, 1939, and *M. bramkampi* Clark and Anderson, 1938. One West Coast species, *Bullia* (*Buccinanops*) *clarki* Wagner and Schilling, 1923 appears to be related to living species of *Bullia* (*Buccinanops*) from southern South America, and is retained in this genus and subgenus. The morphological features supporting these conclusions are discussed under each species.

For reasons given in the discussion of the type species, the genus name *Molopophorus* Gabb, 1869 may be unavailable, at least for species believed to be related to the *Bullia* group. For convenience, and pending further study and a thorough revision of these taxa, all are here discussed under "*Molopophorus*".

Genus **MOLOPOPHORUS** Gabb, 1869

Type species (by original designation).—*Molopophorus striatus* (Gabb, 1869).

"**Molopophorus**" **striatus** (Gabb)

Bullia (*Molopophorus*) *striata* Gabb, 1869, p. 157, pl. 26, fig. 36; Tryon, 1882, p. 7, pl. 3, fig. 27; Tryon, 1883, p. 156, pl. 52, fig. 80.

Molopophorus striatus (Gabb). Dall, 1909, p. 45; Dickerson, 1915, p. 67, pl. 8, fig. 6; Anderson and Hanna, 1925, p. 44, 72, 74, pl. 8, fig. 14.

Molopophorus striatus (Gabb). Fischer, 1884, p. 634; Clark, 1921, p. 159 [in part]; Stewart, 1927, p. 389, pl. 29, fig. 14; Keen and Bentson, 1944, p. 173.

Occurrence.—California, Tejon Formation.

Range.—Upper Eocene.

Type locality.—Unknown, given by Gabb as "Tejon, California".

Material examined.—Lectotype, ANSP 4249; Hypotype, UCMP 30750.

Remarks.—The status of *M. striatus* is problematic. Nuttall and Cooper (1973) claim that it lacks a terminal columellar fold. This opinion, however, is based mainly on external comparison with *Brachysphingus gibbosus* Nelson, 1925 which *M. striatus* closely resembles, and which upon sectioning shows no columellar fold. The columellae of both the lectotype and a hypotype of *M. striatus* are complex, and could perhaps be said to bear terminal plaits. The small size of these specimens makes unambiguous determination difficult without sectioning. The prominence of axial sculpture and the form of growth lines may ally this species with some other species assigned to *Molopophorus*, while its short spire and inflated body whorl distinguish it from most of these forms.

If *M. striatus* is in fact a juvenile of a species of *Brachysphingus*, then the generic name *Molopophorus* is a junior synonym of *Brachysphingus* and unavailable. If the specimens are adults, but non-nassariid, then none of the several species suggested below as possibly related to the *Bullia* group can be referred to the genus *Molopophorus*. It is therefore likely that most the the species discussed below will eventually be placed in one or more genera other than *Molopophorus*.

"**Molopophorus**" **anglonanus** (Anderson)
Plate 10, figures 1a, 1b, 4

Bullia (*Molopophorus*) *anglonana* Anderson, 1905, p. 205, pl. 16, fig. 74–76; Anderson, 1911, p. 100.

Molopophorus anglonana (Anderson). Etherington, 1931, pp. 97–98, pl. 13, figs. 1, 2, 4, 5, 7, 10, 14–16; Weaver, 1942, p. 470, pl. 90, figs. 14–16, 18, 23; Hanna and Hertlein, 1943, p. 174, figs. 64–14; Moore, 1963, pp. 37–38, pl. 3, figs. 1, 4.

(?) *Molopophorus* cf. *M. anglonana* (Anderson). Moore, 1963, p. 38, pl. 3, fig. 5.

Molopophorus anglonanus (Anderson). Keen and Bentson, 1944, p. 135; Addicott, 1965a, p. C106, fig. 4L; Addicott, 1970, pp. 95–96, pl. 11, figs. 1–4.

Occurrence.—California, Monterey Shale; Washington, Astoria Formation; Oregon, Emporia Formation.

Range.—Lower–middle Miocene.

Type locality.—Kern River, Kern County, California.

Material examined.—Neotype, CAS 91; Hypotypes, UCMP 32016, 32018, 32019.

Other types.—Holotype lost [*fide* Weaver, 1942, p. 471]; Plesiotypes, UCMP 32020, 32021, 32023, 32025, 32026.

Remarks.—With its noded to spinose shoulders, this is one of the most distinctive species assigned to *Molopophorus*. Weaver (1942) observed that there is significant variation in the degree of development of axial ribbing and spination. The ontogenetic series he illustrates suggests that younger individuals display more pronounced longitudinal ribs, while adults display little or no axial sculpture other than spiral rows of knobs, tubercles, or spines. This is also apparent from examination of the type specimens listed above. The largest individuals clearly display a pronounced terminal columellar fold and well-developed reflected siphonal channel around the fasciole. In overall form it most closely resembles *M. gabbi* Dall, 1909 and, to a lesser degree, *M. dalli* Anderson and Martin, 1914. All three forms show similar overall shell morphology, pronounced shouldering, at least incipient tuberculated sculpture, and a somewhat "bottom-heavy" shape, caused by swelling of the anterior half of the body whorl.

Concerning the distribution of *anglonanus*, Addicott (1970, p. 96) states that, "Despite its wide geographic range during the Miocene, *Molopophorus anglonanus* is definitely known from only four limited areas along the Pacific coast. It is noteworthy," he adds, "that the California occurrences are limited to the east side of the San Andreas fault."

"**Molopophorus**" **matthewi** Etherington
Plate 10, figure 7

Molopophorus anglonana (Anderson) var. *matthewi* Etherington, 1931, pp. 98–99, pl. 13, figs. 3, 6, 8, 9, 13; Weaver, 1942, p. 471, pl. 90, figs. 17, 19.

Molopophorus anglonana matthewi Etherington. Moore, 1963, p. 38, pl. 3, fig. 7.

Molopophorus matthewi Etherington. Plafker and Addicott, 1976, p. 21.

Occurrence.—Washington, Astoria Formation; Alaska (?), Yakataga Formation.

Range.—Lower–middle Miocene.

Type locality.—Grays Harbor County, Washington (UW loc. 416).

Material examined.—Holotype, UCMP 32028.

Remarks.—Although he listed it as a variety of *M. anglonanus* (Anderson, 1905), Weaver (1942) believed that *matthewi* was more closely related to *M. clarki* (Weaver, 1912) and *M. fishii* (Gabb, 1869) than to *M. anglonanus* s. s. Moore (1963, p. 38) ventured that *matthewi* "should perhaps be considered of specific rather than subspecific rank," and stated that *M. anglonanus* is "sufficiently variable to include the subspecies *matthewi*." Addicott (1970, pp. 95–96) followed this latter opinion and considered *matthewi* a subspecies of *anglonanus*. The holotype shares with *anglonanus* similar overall dimensions and a swollen body whorl. However, it lacks any of the pronounced tuberculation that is so conspicuous in larger specimens of *anglonanus*. The siphonal channel around the fasciole is well developed, and there appears to be a columellar fold, although this feature is perhaps not as noticeable as on specimens of *anglonanus*.

"**Molopophorus**" **gabbi** Dall

Molopophorus gabbi Dall, 1909, p. 45, pl. 3, fig. 8; Anderson and Martin, 1914, p. 78, pl. 6, figs. 5a, b; Weaver, 1942, pp. 466–467, pl. 90, figs. 4, 6; Durham, 1944, p. 170, pl. 18, fig. 5; Moore, 1976, pp. 35–36, pl. 5, figs. 1–22.

Molopophorus biplicatus gabbi Clark, 1918, p. 174, pl. 6, figs. 7a, b.

Occurrence.—Oregon, Pittsburg Bluff Formation, Gries Ranch Formation, Tunnel Point Sandstone, Quimper Sandstone; Washington, Lincoln Creek Formation; California, San Lorenzo Formation.

Range.—Lower–middle Oligocene, possibly upper Eocene–lower Miocene.

Type locality.—Pittsburg, Columbia County, Oregon (UW loc. 500).

Material examined.—Lectotype, USNM 107377; Syntypes, USNM 214015, 214016.

Remarks.—Weaver (1942, p. 466) stated that this species is similar to *M. dalli* Anderson and Martin, 1914, but is distinguished by the presence of two frequently noded spiral carinae, faintly developed spiral ribbing, a more elongate anterior canal, and "a smaller surface on the body whorl between the upper carina and suture." In its tuberculated sculpture, *gabbi* superficially resembles adult specimens of *M. anglonanus* (Anderson, 1905). It displays two rows of tubercles around the midsection of the body whorl, however, while *anglonanus* shows only one, albeit more pronounced. The columella of *gabbi* appears to bear something of a terminal columellar fold and a pair of spiral ridges bordering a siphonal channel, in these features

also resembling *anglonanus*. It differs from this species in its rounder, more evenly inflated form and apparently smaller adult size. Based on the large number of specimens figured by Moore (1976), it is clear that expression of both axial and spiral sculpture is variable in this species. Moore, in fact, claims this variability to be the most distinctive character of the species. Some specimens have an almost cancellated appearance, while others show only axial ribs and others only spiral ribs. More constant features include the depressed, unsculptured area comprising the upper one-third to one-half of the body whorl, the angulation of the whorl profile at the sutures, the relatively short anterior canal with a sharp ridge at its posterior margin, the overall shell form of stocky body whorl and low, frequently almost button-like spire, and the presence of spiral ridges without longitudinal elements on the anterior portion of the body whorl.

"Molopophorus" biplicatus (Gabb)
Plate 10, figure 6

Cuma biplicata Gabb, 1866, p. 9, pl. 2, fig. 14; Gabb, 1869, p. 75; Dall, 1890, p. 155; Dall, 1896, p. 463; Arnold, 1906, p. 19, 79; Arnold, 1907, p. 530; Arnold, 1908, p. 350; Arnold, 1909, p. 4; Anderson, 1911, p. 100; Anderson and Martin, 1914, p. 43.

Cuma biplicata var. *quadranodosum* Weaver, 1912, pp. 75–76, pl. 11, figs. 91–93, pl. 14, fig. 122.

Molopophorus biplicata (Gabb). Merriam and Clark *in* Lawson, 1914, p. 10.

Molopophorus biplicatus (Gabb). Clark, 1915, pp. 15, 20; Clark, 1918, pp. 80, 91, 97, 174, pl. 20, figs. 4, 6, 8; Stewart, 1927, pp. 389–390, pl. 31, fig. 4; Keen and Bentson, 1944, p. 172.

Molopophorus biplicatus var. *quadranodosum* (Weaver). Weaver, 1942, p. 469.

Occurrence.—California, San Ramon Sandstone; Washington, horizon unknown (middle Oligocene).

Range.—Middle Oligocene–lower Miocene (?).

Type locality.—(*C. biplicata*) probably south of Martinez, Contra Costa County, California; (var. *quadranodosum*) branch of Wilson Creek, Wahkiakum County, Washington.

Material examined.—Lectotype (*C. biplicata*), ANSP 4340; non-type material, MCZ(IP) 27898, 27846 [total: four specimens].

Other types.—Holotype of *M. b. quadranodosum*, UW 76 [lost, *fide* Weaver, 1942, p. 469].

Remarks.—Clark (1918, p. 174) considered *M. biplicatus* to be so similar to *M. gabbi* Dall, 1909 that he suggested that *gabbi* be considered a subspecies of *biplicatus*. Moore (1976, p. 35) observed that the lectotype specimen of *biplicatus* has a less inflated body whorl and a higher spire than *gabbi*, and lacks the unsculptured subsutural concavity characteristic of *gabbi*. The latter may be the most consistent feature distinguishing the two forms.

"Molopophorus" dalli Anderson and Martin
Plate 10, figures 2, 3

Molopophorus dalli Anderson and Martin, 1914, p. 78, pl. 6, figs. 7a, b; Wagner and Schilling, 1923, p. 259, pl. 50, fig. 1; Weaver, 1942, p. 469, pl. 90, fig. 8; Durham, 1944, p. 170; Keen and Bentson, 1944, p. 172; Hickman, 1969, p. 91, pl. 13, fig. 1.

Occurrence.—Oregon, Eugene Formation, Quimper Sandstone; California, San Emigdio Formation.

Range.—Lower–middle (?) Oligocene.

Type locality.—San Emigdio region, Kern County, California.

Material examined.—Holotype, CAS 168; Paratype, CAS 169; Hypotype, UCMP 30633; non-type material, UCMP stratigraphic collection, Loc. A-1606 [total: eight specimens].

Other types.—Hypotype, UO 27399.

Remarks.—This is a large form, characterized by a relatively inflated body whorl, reduced expression of axial sculpture, and pronounced angulation of the whorl at the sutures. Weaver (1942) and Hickman (1969) both have suggested that *dalli* is most similar to *M. gabbi* Dall, 1909, differing mainly in the more pronounced nodes or tubercles on the latter and spiral ribbing on the former.

"Molopophorus" newcombei (Merriam)

Nassa (?) n. sp. Merriam, 1896, p. 106.

Nassa newcombei Merriam, 1897, p. 63; Merriam, 1899, p. 179, pl. 23, fig. 3.

Alectryon [*sic*] *newcombei* (Merriam). Arnold and Hannibal, 1913, p. 576.

Molopophorus newcombei (Merriam). Clark and Arnold, 1923, pp. 160–161, pl. 31, figs. 8a, b; Weaver, 1942, p. 467, pl. 90, fig. 5; Durham, 1944, p. 171.

Occurrence.—British Columbia, Sooke Formation.

Range.—Upper Oligocene–lower Miocene.

Type locality.—West of Otter Point, Sooke Bay, Vancouver Island.

Types.—Unknown.

Material examined.—None.

Remarks.—Weaver (1942) stated that this species "is characterized by its relatively high spire, comparatively slender shape, the prominent spiral groove and collar above it just beneath the suture, the numerous longitudinal ribs on spire and on upper half of body whorl which fade out and disappear on the lower half, and the faintly developed spiral ribs on upper half of body whorl." Weaver's figured specimen displays a markedly twisted columella which appears to bear a terminal fold.

"Molopophorus" lincolnensis Weaver
Plate 10, figure 5

Molopophorus lincolnensis Weaver, 1916, p. 50, pl. 4, figs. 60, 61; Weaver, 1942, pp. 467–468, pl. 90, fig. 7; Durham, 1944, p. 170.

Molopophorus lincolnensis weaveri Durham, 1944, pp. 170–171, pl. 15, fig. 18.

Occurrence.—Washington, Lincoln Creek Formation.

Range.—Upper Eocene–lower Miocene.

Type locality.—Galvin Station, Lewis County, Washington (UW loc. 256).

Material examined.—Holotype of *M. lincolnensis*, CAS 467; Holotype of *M. l. weaveri*, UCMP 35370; non-type material of *M. lincolnensis*, UCMP stratigraphic collection, Locs. A-9, A-1632, A-1633, A-1634 (Lewis and Thurston counties, Washington) [total: 270 specimens].

Other Types.—Syntype, UW 113.

Remarks.—This moderately sized form is very abundant in the Lincoln Creek Formation of Washington. Spiral sculpture is almost completely lacking, the entire shell usually being covered with moderately pronounced axial ribs. These vary among individuals, but are often most prominent over the middle of the body whorl. A terminal columellar fold is moderately pronounced. In general form and proportions *lincolnensis* is very similar to *Colwellia bretzi* (Weaver, 1912), and may be referable to that genus.

"Molopophorus" bogachielii (Reagan)

Buccinum bogachielii Reagan, 1909, p. 218, pl. 5, figs. 51a, b.
Molopophorus bogachieli [*sic*] (Reagan). Addicott, 1976, pp. 105, 110, pl. 3, fig. 13; Addicott, 1978, pp. 680, 682, figs. 5c–5e.
Molopophorus cf. *M. bogachielii* (Reagan). Marincovich, 1983, pp. 116–117, pl. 23, figs. 5–7.

Occurrence.—Oregon, Empire Formation; Washington, Quillayute Formation, Montesano Formation; British Columbia, Skonun Formation; Alaska, Tachilni Formation.

Range.—Upper Miocene.

Type locality.—Olympic Peninsula, Washington (USGS loc. 10127).

Material examined.—Holotype, USNM 328362; Hypotypes, USNM 245656, 245657, 245658.

Other types.—Hypotypes, UA 2495, 2496.

Remarks.—This species differs from others assigned to *Molopophorus* in being narrower and more elongate, and in showing little or no external sculpture. Alaskan specimens of this species figured by Marincovich bear four columellar folds. Whether this represents a significant distinction from southern species is unclear, as the columella is unknown for most species. *M. bogachielii* appears to show a well-developed siphonal channel on the fasciole. While being rather high-spired, this species resembles species assigned to the *Bullia* group in overall shell form. It differs from most, but not all, of these species in its total lack of spiral sculpture and the presence of pronounced multiple columellar folds. One specimen figured by Marincovich (UA 2496) appears to show a terminal columellar fold. *M. bogachielii* is an important index species in Washington, Oregon, and Alaska (Marincovich, 1983).

"Molopophorus" crooki Clark

Molopophorus crooki Clark, 1938, p. 715, pl. 4, figs. 14, 37, 43, 45, 46.

Occurrence.—California, Markley Formation.

Range.—Upper Eocene.

Type locality.—Solano County, California (UCMP loc. A-1297).

Material examined.—Holotype, UCMP 30746 (Solano County, California).

Other types.—Paratypes, UCMP 30742, 30747 (Solano County, California).

Remarks.—Clark suggested that *M. crooki* most closely resembles *M. tejonensis* Dickerson, 1915[29], differing mainly in being more elongate and slender, having less convex whorls, less pronounced but more numerous axial and spiral ribs, and two instead of four carinae or plications on the columella. A terminal columellar fold is more problematic in *crooki* than in *tejonensis*, and the aperture of the former is narrower and its outer lip less flared than the latter.

"Molopophorus" clarki (Weaver)
Plate 10, figure 11

Brachysphingus clarki Weaver, 1912, p. 48, pl. 4, fig. 38, pl. 6, fig. 57.
Molopophorus clarki (Weaver). Weaver, 1942, p. 468, pl. 90, fig. 12.

Occurrence.—Washington, Cowlitz Formation.

Range.—Upper Eocene.

Type locality.—Olequa Creek, Lower Cowlitz Valley, Washington (UW loc. 5).

Material examined.—Holotype, CAS 494.

Remarks.—This form is not to be confused with *Bullia* (*Buccinanops*) *clarki* Wagner and Schilling, 1923, discussed on p. 70, although the two do show some superficial similarities. The columellar and fasciolar regions in both forms are relatively simple, tapering to a point rather than to an oblique fold. Neither shows any external sculpture aside from growth lines, and they have very similar overall shapes. They differ, however, in the columella of *B. clarki* being slightly "flexed" anteriorly, with a slight terminal fold. The anterior notch of *B. clarki* is relatively shallower, although this could be due to breakage of the specimen examined (UCMP 11430). The columella of *M. clarki* is more or less straight, tapering to a distinct point similar to that in *M. fishii* (Gabb, 1869) (see p. 68) and in species of the "*Bullia*" *altilis* complex of the Gulf coastal plain.

[29] herein *Colwellia tejonensis* (Dickerson).

Neither *B. clarki* nor *M. clarki* show a bordered siphonal channel around the fasciole.

Weaver (1942) and Hickman (1969) have noted strong similarities between *clarki* and *fishii*. Both forms have relatively low spires with that of *clarki* slightly higher than that of *fishii*. Neither shows well-developed spiral or axial sculpture or a pronounced terminal columellar fold. Both forms show pronounced ridges bounding a recurved siphonal channel around the posterior margin of the anterior siphonal notch and fasciole.

"Molopophorus" californicus Clark and Woodford

Molopophorus californicus Clark and Woodford, 1927, p. 117, pl. 20, figs. 16, 17; Keen and Bentson, 1944, p. 172.
Molopophorus californicus lonsdalei Turner, 1938, p. 77, pl. 15, figs. 7, 8; Weaver, 1942, p. 464, pl. 89, fig. 28.

Occurrence.—California, Meganos Formation; Oregon, Umpqua Formation.

Range.—Paleocene–middle Eocene.

Type locality.—Contra Costa County, California.

Material examined.—Holotype, UCMP 31247; Paratype, UCMP 31248; Holotype of *M. c. lonsdalei*, UCMP 33244.

Remarks.—This species is notable for the dominance of axial over spiral sculpture. In overall shape and dimensions it is not unlike some species of the *Bullia* group. Spiral sculpture is restricted to abapical and adapical ends of the body whorl, and is absent from the middle. The anterior end of the columella is damaged in the specimens examined, and the systematic position of this species must thus remain indeterminate for the present.

Turner (1938) described the subspecies *lonsdalei* from the middle Eocene of Oregon. It differs from *californicus* s. s. in the smaller number but greater development of the axial ribs, particularly over the shoulder and sutural regions. Spiral grooves are still present on the subsutural area of the body whorl.

"Molopophorus" bramkampi Clark and Anderson

Molopophorus bramkampi Clark and Anderson, 1938, pp. 951–952, pl. 4, figs. 3, 7, 8; Keen and Bentson, 1944, p. 172,

Occurrence.—California, Wheatland Formation.

Range.—Lower Oligocene.

Type locality.—Yuba County, California.

Material examined.—Holotype, UCMP 11298; Paratype, UCMP 11290.

Remarks.—Clark and Anderson suggested that *bramkampi* is very similar to *Molopophorus bretzi* (Weaver, 1912)[30], differing only in being more inflated and having a less well-developed subsutural band and columellar plicae. It differs more significantly from *bretzi* in general form, having a more truncated anterior canal region, and in its virtual lack of external sculpture.

"Molopophorus" effingeri Weaver

Molopophorus bramkampi Effinger, 1938, p. 383, pl. 47, figs. 1, 10 [*non bramkampi* Clark and Anderson, 1938].
Molopophorus effingeri Weaver, 1942, pp. 465–466, pl. 90, figs. 2, 3; Durham, 1944, p. 170, pl. 18, fig. 11.

Occurrence.—Washington, Gries Ranch Formation.

Range.—Lower Oligocene.

Type locality.—Old Gries Ranch, Lower Cowlitz Valley, Washington (UW loc. 239).

Material examined.—Holotype, UCMP 33592.

Remarks.—Clark and Anderson's description of *Molopophorus bramkampi* was published in June of 1938. Effinger's description of a very different form under the same name appeared in July of the same year, and is therefore a homonym. Weaver (1942) proposed the name *effingeri* for Effinger's high-spired species.

Weaver stated that *effingeri* is most similar to *Molopophorus bretzi* (Weaver, 1912)[31], "but differs in having a relatively higher spire, two more whorls to the spire, a more depressed suture, and slightly shorter anterior canal." The differences, however, would appear to be much more profound than he suggests. Few nassariids in or out of the *Bullia* group have so high a spire or such deep sutures. The presence of both a terminal columellar fold and siphonal channel around the fasciole are problematic on the holotype.

"Molopophorus" fishii (Gabb)
Plate 10, figure 15

Ancillaria fishii Gabb, 1869, p. 9, pl. 2, fig. 15.
Bullia buccinoides Merriam, 1899, p. 179, pl. 23, fig. 5.
Ancilla fishii (Gabb). Clark, 1918, p. 185, pl. 19, fig. 4; Clark and Arnold, 1923, p. 161, pl. 31, figs. 9a, b, 10a, b; Keen and Bentson, 1944, p. 129.
Molopophorus fishii (Gabb). Weaver, 1942, p. 470, pl. 90, figs. 9–11; Durham, 1944, p. 170; Hickman, 1969, pp. 90–91, pl. 13, figs. 2–5.

Occurrence.—California, San Ramon Formation, British Columbia, Sooke Formation; Oregon, Eugene Formation, Yaquina Formation.

Range.—Middle–upper Oligocene.

Type locality.—Northwest of Walnut Creek, Contra Costa County, California.

Material examined.—Syntype of *Bullia buccinoides*, UCMP 11929.

Other Types.—UO 27394, 27395, 27396, 27397, 27398; Hypotypes, UCMP 11248, 31173, 11249,

[30] herein *Colwellia bretzi* (Weaver).

[31] herein *Colwellia bretzi* (Weaver).

32457; Holotype of *A. fishii* Gabb, 1869 missing [*fide* Keen and Bentson, 1944, p. 130).

Remarks.—Based on a comparison of Merriam's type specimen with published figures of *fishii*, it appears reasonable to synonymize *Bullia buccinoides* with *M. fishii*. Clark and Arnold (1923) make no mention of the former taxon in their summary of the Sooke fauna.

M. fishii may be distinguished from most other species assigned to *Molopophorus* by its smooth, globular shape, and virtual lack of external shell sculpture. As already noted, however, it shares these and other features with *M. clarki*. The terminal portion of the columella is relatively simple, tapering evenly to a point, and the presence of a terminal fold is problematic. The form of the aperture and columella, and almost total lack of external sculpture ally this species to members of the "*Bullia*" *altilis* complex from the Gulf coastal plain Eocene. It does not appear to be a nassariid.

"Molpophorus" stephensoni Dickerson

Molopophorus stephensoni Dickerson, 1917, p. 177, pl. 30, figs. 10a, b; Effinger, 1938, p. 383; Weaver, 1942, p. 465, pl. 90, fig. 1; Durham, 1944, p. 171, pl. 18, fig. 1.
Molopophorus cf. *stephensoni* Dickerson. Clark and Anderson, 1938, p. 952, pl. 3, fig. 15.

Occurrence.—Washington, Gries Ranch Formation; California,Wheatland Formation.

Range.—Lower Oligocene.

Type locality.—Old Gries Ranch, Lewis County, Washington (UW loc. 239).

Material examined.—Holotype, CAS 422; Paratype, CAS 423.

Other types.—Hypotype of *M.* cf. *stephensoni*, UCMP 11270.

Remarks.—Weaver (1942) wrote that *stephensoni* "is characterized by its high spire, and fine, cancellate sculpture on posterior whorls of spire." The columella of the holotype resembles that of *M. anglonanus* (Anderson, 1905) and suggests that *stephensoni* may be a nassariid. Its small size, relatively elongate siphonal canal, and particularly its cancellate sculpture, however, dissociate it from the *Bullia* group.

"Molopophorus" aequicostatus Vokes

(?) *Nassa packardi* Weaver. Dickerson, 1916, pp. 433, 451.
Molopophorus aequicostatus Vokes, 1939, p. 143, pl. 19, fig. 5.

Occurrence.—California, Domengine Formation.

Range.—Middle Eocene.

Type locality.—Fresno County, California (UCMP loc. 672).

Material examined.—Holotype, UCMP 15941.

Remarks.—Vokes stated that *aequicostatus* was characterized by the equally developed spiral and axial sculpture, forming nodes at their intersections. This form shows a number of features which suggest that it is not closely related to the *Bullia* group. In its fine cancellate sculpture it resembles some species of nassariines, but within the "*Molopophorus*" group only *M. stephensoni* Dickerson, 1917. This sculpture is almost homogeneous over the entire shell. The form of the columella is problematic on the holotype, but may allow *aequicostatus* to be referred to Nassariidae.

Genus COLWELLIA Nuttall and Cooper, 1973

Type species.—*Colwellia flexuosa* (Edwards, 1866).

Colwellia bretzi (Weaver)

Ancillaria bretzi Weaver, 1912, p. 53, pl. 2, fig. 21.
Molopophorus bretzi (Weaver). Weaver, 1942, pp. 464–465, pl. 89, fig. 22.
Colwellia bretzi (Weaver). Nuttall and Cooper, 1973, pp. 208–209.

Occurrence.—Washington, Cowlitz Formation; Oregon, Arago Formation.

Range.—Upper Eocene.

Type locality.—East of Vader, Lower Cowlitz Valley, Washington (UW loc. 232).

Material examined.—Syntypes, CAS 500, 500a, 500b; non-type material, UCMP stratigraphic collection, loc. D-3318 (Coos County, Oregon) [total: four specimens].

Other types.—Hypotypes, BM(NH) GG 12783/1, 12783/2.

Remarks.—Weaver (1942) noted that this form is characterized "by its relatively small size, lack of spiral ribs, and by a plication on the anterior portion of the columella between the siphonal fasciole and the margin of the canal." In their revision of European species formerly assigned to *Cominella*, Nuttall and Cooper (1973) assigned to their new genus *Colwellia* "only those American species which have a very strong resemblance to *C. flexuosa* [(Edwards, 1866)] and *C. auversiensis* [(Deshayes, 1865)]." The four American species referred to *Colwellia* differ from others assigned to *Molopophorus* in the combination of a uniform, fusiform shape without angulations, noding, or shouldering, relatively short spires, generally subdued sculpture, and well-developed terminal columellar folds.

Colwellia tejonensis (Dickerson)
Plate 10, figure 13

Molopophorus tejonensis Dickerson, 1915, pp. 66–67, pl. 8, figs. 3a, b; Clark, 1938, p. 715, pl. 4, figs. 38, 39, 47; Keen and Bentson, 1944, p. 173; Givens, 1974, p. 84, pl. 10, fig. 2.
Cominella tejonensis (Dickerson). Anderson and Hanna, 1925, p. 72.
Colwellia tejonensis (Dickerson). Nuttall and Cooper, 1973, pp. 208–209.

Occurrence.—California, Tejon Formation, Juncal

Formation, Matilija Formation; Washington, Cowlitz Formation; Oregon, Coaledo Formation.

Range.—Upper Eocene.

Type locality.—Kern County, California.

Material examined.—Holotype, CAS 320; non-type material, UCMP stratigraphic collection, loc. A-858 (Coos County, Oregon) [total: five specimens].

Remarks.—In describing *Molopophorus tejonensis*, Dickerson noted similarities to *M. striatus* (Gabb, 1869), and suggested that further study might show that *tejonensis* is actually an adult of *striatus*. Larger collections than are now available will be necessary to test this suggestion. Stewart (1927) listed *M. tejonensis* as a synonym of *M. cretaceus* (Gabb, 1864). Clark (1938) noted, however, that these two forms differ in both the number of longitudinal ribs and the degree of whorl convexity.

Colwellia antiquata (Gabb)
Plate 10, figures 8–10

Nassa antiquata Gabb, 1864, p. 97, pl. 18, fig. 50.
Molopophorus antiquatus (Gabb). Stewart, 1927, pp. 390–391, pl. 28, fig. 4; Turner, 1938, p. 77, pl. 15, fig. 11; Vokes, 1939, p. 142, pl. 19, figs. 1–3; Weaver, 1942, pp. 463–464, pl. 89, figs. 31, 32, pl. 103, fig. 12; Givens, 1974, p. 84, pl. 10, fig. 1.
Colwellia antiquata (Gabb). Nuttall and Cooper, 1973, pp. 208–209.

Occurrence.—Oregon, Umpqua Formation; California, Juncal Formation.

Range.—Lower Eocene–upper middle Eocene.

Type locality.—Kings County, California (UCMP loc. A819).

Material examined.—Holotype, ANSP 4198; Hypotypes, UCMP 15938, 15939, 15940, 30750, 33246.

Remarks.—Stewart (1927) suggested that *antiquatus* might be a variety or more mature specimen of *M. cretaceus* (Gabb, 1864). Vokes (1939) rejected this idea on the grounds that at least one apparently immature specimen showed features distinctive of *antiquatus*. Weaver (1942) stated that this species was related to but could be distinguished from *bretzi* (Weaver, 1912) "by the presence of moderately developed fine spiral ribs," and also by its more impressed sutures. Givens (1974) has suggested that *antiquata* may be ancestral to *tejonensis* (Dickerson, 1915).

Colwellia cretacea (Gabb)

Nassa cretacea Gabb, 1864, p. 97; Gabb, 1869, p. 219; Dickerson, 1916, pp. 433, 451.
"*Nassa*" *packardi* Weaver, 1912, p. 43, pl. 3, fig. 34.
Molopophorus cretaceus (Gabb). Stewart, 1927, p. 391, pl. 28, fig. 9; Vokes, 1939, pp. 141–142, pl. 19, fig. 4; Keen and Bentson, 1944, p. 172; Squires, 1984, p. 31, fig. 8f.
Colwellia cretacea (Gabb). Nuttall and Cooper, 1973, pp. 208–209.

Occurrence.—California, Domengine Formation, Llajas Formation.

Range.—Middle Eocene.

Type locality.—Bull's Head Point, Contra Costa County, California.

Material examined.—Lectotype, ANSP 4197.

Remarks.—Clark (1938, p. 716) suggested that *Molopophorus antiquatus* (Gabb, 1864) should be considered a synonym of *M. cretaceus*, noting that the "ribbing and outline of the two forms are similar," and that they "apparently come from the same beds (middle Eocene, Bull's Head Point), near the town of Martinez, Contra Costa County." Vokes tentatively suggested that a form described as *Nassa packardi* by Weaver (1912) from the Cowlitz Formation of Washington might be referable to this species. Acceptance of this suggestion would involve both stratigraphic and geographic range extensions for the species.

Genus **BULLIA** Gray *in* Griffith and Pidgeon, 1834

Type species.—*Bullia semiplicata* Gray, 1834.

Subgenus **BUCCINANOPS** d'Orbigny, 1841

Type species.—*Buccinum globulosum* Kiener, 1834.

Bullia (Buccinanops) ? clarki Wagner and Schilling
Plate 10, figure 12

Bullia (*Buccinanops*) *clarki* Wagner and Schilling, 1923, p. 259, pl. 50, figs. 2–5; Keen and Bentson, 1944, p. 135; Cernohorsky, 1982, p. 17-238.
Bullia clarki wheatlandensis Clark and Anderson, 1938, p. 951, pl. 4, figs. 9–12; Keen and Bentson, 1944, p. 135.
Buccinanops clarki (Wagner and Schilling). Schenk and Keen, 1940, pl. 29, fig. 6.

Occurrence.—California, San Emigdio Formation, Wheatland Formation.

Range.—Middle–upper Oligocene.

Type locality.—San Emigdio Grant, Mt. Pinos quadrangle, Kern County, California.

Material examined.—Holotype of *B. clarki*, UCMP 11430; Paratype, UCMP 11429; Holotype of *B. c. wheatlandensis*, UCMP 11299; Paratype, UCMP 11300.

Remarks.—This form shows a number of characters which support its placement in *Buccinanops*. It is similar to living species of *Buccinanops* in overall form and dimensions; the spire is relatively short, the body whorl inflated and evenly rounded. Axial sculpture consists only of growth lines. The aperture is simple and similar to that of several living species. The parietal callus is prominent but restricted in extent, and shows a smooth margin along the body whorl. There is a slight subsutural shouldering on the body whorl. The anterior canal is slightly elongated, and the columella bears a terminal fold. One possibly interesting feature of one specimen (UCMP 11300) is the slight adapical flaring of the posterior end of the aperture, a

feature also shown by *Calophos baranoanus* (Anderson, 1929) from the Neogene of Ecuador, discussed on p. 76.

Hickman (1980, p. 58, pl. 7, fig. 15) tentatively assigned two incomplete neogastropod specimens from the upper Paleogene Keasey Formation of Oregon to *Bullia clarki*. She noted, however, that these specimens differed from *clarki* in having a higher spire, more well-developed spiral sculpture, and a thicker outer lip. Her figured specimen (USNM 251394) is completely covered by coarse spiral ribbing. Its apex and anterior columella are missing, preventing any definite conclusion, but I suggest that it does not belong to *Bullia* (*Buccinanops*) *clarki*.

CENOZOIC OF THE CARIBBEAN, CENTRAL AND NORTHERN SOUTH AMERICA

Four groups of species from Cenozoic deposits of the Caribbean basin have been allied with the *Bullia* group. The first includes two forms from the Eocene of Peru, assigned to the genus *Dorsanum* Gray, 1847 by Olsson (1928). The second includes a large number of species previously assigned to several different genera but here included in the genus *Calophos* Woodring, 1964. The third includes at least one species probably assignable to *Buccinanops* d'Orbigny, 1841, and the fourth a poorly defined group of uncertain position, *Perunassa* Olsson, 1932.

Genus **DORSANUM** Gray, 1847

Type species.—*Buccinum politum* Lamarck, 1822.

"**Dorsanum**" **parinense** (Olsson)
Plate 13, figures 1, 2

Dorsanum parinense Olsson, 1928, pp. 83–84, pl. 18, figs. 5, 6; Cernohorsky, 1982, p. 17-239.

Occurrence.—Peru, Parinas Formation.
Range.—Middle Eocene.
Type locality.—Keswick Hills, Peru.
Material examined.—Holotype, PRI 3666; Paratype, PRI 3667.
Remarks.—(see below, under "*Dorsanum*" *lagunitense*.)

"**Dorsanum**" **lagunitense** (Woods)
Plate 13, figures 3, 4

Nassa lagunitensis Woods, 1922, p. 95, pl. 12, fig. 12, pl. 13, fig. 1.
Dorsanum lagunitense (Woods). Olsson, 1928, pp. 83–84.

Occurrence.—Peru, Restin Formation, Saman Formation.
Range.—Upper Eocene.
Type locality.—Lagunitas, Peru.
Material examined.—None.
Types.—Unknown.
Remarks.—In describing *Dorsanum parinense*, Olsson (1928) suggested that it was a logical ancestor for *Nassa lagunitensis* Woods, 1922 from the middle to upper Eocene "Lobitos Formation" of Peru [= Restin Formation, in part, and Saman Formation of Olsson (1928)], and he favored including *lagunitensis* in *Dorsanum* as well. From *lagunitensis*, Olsson observed, *parinense* "differs by its smaller size, the last whorl is less evenly convex and the base sharply contracted so that in contour, the form is quadrate." Both forms, Olsson wrote, "differ from *Bullia* Gray, in having the sutures distinct and free from a cover of enamel." He also reported apparent increase in size in *lagunitensis* within the stratigraphic section examined[32]. "Except in matter of size", noted Olsson, "there is no other change of importance."

The information presently available is insufficient for a positive determination of affinity of these Peruvian forms. In a number of characters they resemble both the Recent species *Dorsanum miran* (Bruguière, 1789) and species from the West Coast of North America allied to the *Bullia* group and usually referred to the genus *Molopophorus* Gabb, 1869 (see p. 63). All of these gastropods are of approximately the same size, although several West Coast forms are somewhat larger. In their lack of conspicuous external sculpture, the Peruvian forms more closely resemble *D. miran* than they do the variable West Coast species. All three groups show the reflexed siphonal channel leading dorsally around the fasciole. Unfortunately, protoconchs are known for neither the Peruvian nor most of the West Coast forms. On the basis of geography, it is reasonable to suggest that the two Peruvian forms represent the southernmost representatives of the *Colwellia*/"*Molopophorus*" group, and they may be congeneric with some of these species.

Genus **CALOPHOS** Woodring, 1964

Type species (by original designation).—*Calophos ectyphus* Woodring, 1964.

In 1964, Woodring described the genus *Calophos* from the lower and middle parts of the Gatun Formation (upper Miocene–lower Pliocene) of Panama, and suggested that a number of previously described and undescribed species from the Caribbean area, including some attributed to the genus *Dorsanum* Gray,

[32] Specimens from the basal Saman Formation (upper middle to lower upper Eocene) averaged approximately 20 mm. Woods' specimens came from stratigraphically higher horizons than Olsson's and measured 30–32 mm in height. At the top of the Saman Formation (upper upper Eocene), the average height was greater still, with specimens commonly over 40 mm.

1847, might be assignable to this taxon. Woodring described the genus as follows:

> Moderately large, somewhat slender to strongly inflated, sutural area of late whorls flat or distinctly constricted. Protoconch 1¼–2½ whorled. End of protoconch marked by appearance of finely reticulate sculpture. Axial sculpture disappearing on fourth to sixth sculptured whorl, or disappearing and reappearing on last few whorls. Spiral sculpture continuing, but on mature body whorl strongest in sutural area and on and near siphonal fasciole, generally weak or absent in central part of whorl. Siphonal fasciole moderately inflated, sculptured with spiral threads, limited by a sharp narrow thread. Basal columellar fold strong, followed by a depression. Interior of outer lip bearing narrow ridges extending far into aperture. (Woodring, 1964, p. 262)

This description serves as an adequate diagnosis for the genus as employed here, with the following additional points: (1) Size is variable. Adult total height of species assignable to *Calophos* ranges from approximately 20 to 50 mm; (2) no preserved protoconchs of *Calophos* species from the Gatun Formation were located in the USNM collections to confirm Woodring's description of the apex. Scanning electron micrographs of a well-preserved specimen of *Calophos wilsoni*, n. sp. from the Pliocene of Florida (Pl. 12, figs. 11, 12) show a protoconch (P1 + P2) of 1¼–1½ whorls measuring approximately 475μm in diameter with a relatively sharp boundary between protoconch and teleoconch. Such a larval shell is well within the range of nonplanktotrophic species, suggesting this mode of development for at least this species of *Calophos*; (3) the presence and expression of striations or ridges inside the aperture are variable.

Woodring placed *Calophos* in Buccinidae, suggesting that in "features of protoconch, siphonal fasciole and aperture" it was similar to the buccinid *Cymatophos* Pilsbry and Olsson, 1941. Reexamination of Woodring's specimens, however, does not support this suggestion. Aside from the difference in sculpture that he noted, there are significant differences between these two genera that seem to link *Calophos* with the *Bullia* group of Nassariidae.

Species of *Cymatophos* [see Pl. 12, fig. 3] superficially resemble species assignable to *Calophos* in certain elements of sculpture and overall shape. *Cymatophos*, however, is clearly more closely connected to other "*Phos*-group" taxa such as *Antillophos* Woodring, *Northia* Gray, 1847 (Pl. 12, fig. 2), *Metaphos* Olsson, 1964, and *Phos* Montfort, 1810 (Pl. 12, fig. 4). These taxa are united by well-developed axial and spiral external sculpture that entirely covers the shell in all species, and possession of a terminal columellar fold of a form distinct from that of most if not all nassariids. In species of *Cymatophos*, the anterior end of the columella is usually inflated and covered with a continuation of axial and spiral sculpture from the body whorl. While often bent to the left initially, the columella is almost always bent to the right at the tip. The callus is not extensive but is separated from the body whorl by a slot or groove (in this differing from typical buccinids, and in fact resembling many species of *Nassarius* Duméril, 1806). The interior of the aperture is usually striated and these striations reflect, albeit often indirectly through a relatively thick shell, the spiral sculpture on the exterior. The outer lip is often notched or scalloped. The whorls of the spire are relatively inflated and convex in outline. The sutures are usually relatively deeply incised.

In *Calophos ectyphus* Woodring, 1964, in contrast, the callus usually extends smoothly onto the body whorl. The interior of the aperture is striated, but these striations are not directly reflected in the exterior spiral sculpture of the body whorl; the outer lip of the aperture is smooth. The anterior canal is well-developed but is relatively short and simple and not sharply reflected. The patterns of spiral sculpture agree with those observed in a number of other fossil and living species in the *Bullia* group, especially in the obsolescence of spiral sculpture on the middle portions of the whorls. The fasciole shows a moderate and relatively simple terminal fold.

In summary, it is the combination of a distinctly inflated anterior columella, bearing a terminal columellar fold, a relatively high spire, and the presence of conspicuous axial and spiral sculpture over the entire shell that set *Cymatophos* and its allies apart from species assignable to *Calophos*. It is conceivable that the species of the "*Phos* group" [including *Cymatophos*, *Northia* Gray, 1847, and others; see, *e.g.*, Olsson (1964)] are more closely related to Nassariidae than are other "buccinids"; the morphological differences described here may support such an idea. These taxa will not be discussed further here except to note that a more detailed analysis of their morphological variation might necessitate alteration in the phylogenetic position of *Calophos* within Nassariidae discussed on pp. 107, 108.

All the species assigned to *Calophos* by Woodring (1964; see Pl. 11, fig. 9 herein), as well as the additional forms assigned to the genus herein, are of no older than Mio-Pliocene age (Table 9). The only potential pre-Miocene record of this group is a pair of poorly preserved specimens from the Eocene of the Tonosí area of Panama (Pl. 11, figs. 4, 5 [USNM 434948, 434949]). In their size, overall shape, form of preserved external sculpture, and geographic position, these specimens agree with those of Neogene species of *Calophos* and may represent the ancestors of the group in the Caribbean basin. All species are from the New World, with the possible exception of *Nassa veneris* Faujas de Saint-

Fond, 1817 from the Neogene of Western Europe (see p. 108).

Calophos ectyphus Woodring
Plate 11, figures 1, 2

Calophos ectyphus Woodring, 1964, p. 263, pl. 42, figs. 12, 13, 16, 17.

Occurrence.—Panama, Lower and Middle Gatun Formation.

Range.—Upper Miocene (?)–lower Pliocene.

Type locality.—Transisthmian Highway, central Panama (USGS loc. 16909).

Material examined.—Holotype, USNM 643658; Hypotype, USNM 643659; (holotype lot from USGS

Table 9.—Stratigraphic and geographic distribution of species assignable to the genus *Calophos.*

	Galapagos	Ecuador	Peru	Colombia	Panama	Costa Rica	Mexico	Florida	Dominican Republic	Trinidad
Upper Pliocene	tropicalis oldroydea (1)							wilsoni (12)		
Lower Pliocene		bombax (2) esmereldensis (3)	zorritensis (16)		ectyphus (7)		n.sp. ? (9)			rohri (14)
Upper Miocene				baranoanus (5)	n.sp. ? (6)				golfoyaquensis (13)	
Middle Miocene		ursa (4)					plicatilis (10) mixteca (11)			
Lower Miocene						inornata (8)				
Eocene					n.sp. ? (15)					

* Species first assigned to the genus herein.

[1] **Alectrion tropicalis* Dall and Ochsner, 1928; *Alectrion oldroydae* Dall and Ochsner, 1928.

[2] *Perunassa bombax* Olsson, 1964.

[3] **Gordanops esmereldensis* Olsson, 1964.

[4] *Perunassa* (?) *ursa* Olsson, 1964.

[5] *Phos baranoanus* Anderson, 1929.

[6] (?) *Calophos,* n. sp. (Woodring, 1964, p. 262); specimen USNM 644382 (Pl. 13, fig. 12), specimen from USGS loc. 8345 (Pl. 13, fig. 9), specimen from USGS loc. 8318, all from Boca del Toro area, northwestern Panama.

[7] *Calophos ectyphus* Woodring, 1964.

[8] *Phos inornata* Gabb, 1881.

[9] (?) *Calophos,* n. sp. (Woodring, 1964, p. 262); specimen from USGS loc. 22279, Isthmus of Tehuantepec.

[10] *Cominella plicatilis* Böse, 1906.

[11] *Chrysodomus mixteca* Perrilliat Montoya, 1963.

[12] *Calophos wilsoni,* n. sp.

[13] *Tritia golfoyaquensis* Maury, 1917.

[14] *Phos* (?) *rohri* Rutsch. 1942.

[15] *(?) *Calophos,* n. sp. Specimens USNM 434948, 434949, Tonosi area, Panama (USGS loc. 8426) (Pl. 13, figs. 4, 5).

[16] *(?) *Argobuccinum zorritense* Nelson, 1870.

loc. 16909, hypotype lot from USGS loc. 21956); non-type material from USGS loc. 8435 (Darien, Panama), and USGS locs. 23663, 23664 (Colchoneria, Yero, Panama) [total: 90 specimens].

Remarks.—The type species of *Calophos* is a medium-sized gastropod, not much exceeding 30 mm total height. The spire comprises slightly more than one-third total height. The body whorl is moderately large but not inflated. Sculpture is primarily spiral, with axial elements appearing only on later whorls of some individuals. Variability in shell thickness and sculpture are characteristic of this species, with more or less continuous morphological variation between thick-shelled individuals that show nodes or axial ribs and thinner-shelled, unshouldered specimens showing only spiral sculpture. Almost all individuals show striations on the interior of the outer apertural lip.

Based on Lyellian percentages of molluscan species (proportion of extant species in a fossil fauna), Woodring (1957, p. 47; 1982, pp. 575–576) assigned the Gatun Formation to middle to late (most probably middle) Miocene time. As he pointed out, however (Woodring, 1982, p. 576), this date does not agree with dates derived from microfossils. A date of late Miocene to early Pliocene is indicated by examination of planktonic foraminifera (Bold, 1967; Cronin, 1987, p. 7) from the Gatun; this younger age is accepted by most Recent workers (T. Cronin, T. Collins, oral communs., 1988).

Calophos inornatus (Gabb)
Plate 11, figure 3

Phos inornata Gabb, 1881, p. 338, pl. 44, fig. 2.
Calophos inornatus (Gabb). Woodring, 1964, pp. 262–263.

Occurrence.—Costa Rica, horizon unknown.

Range.—Lower Miocene.

Type locality.—Sapote, Costa Rica.

Material examined.—Syntypes, ANSP 3483 [two specimens].

Remarks.—This species is larger than *C. ectyphus* Woodring, 1964, the types measuring around 35 mm in total height. It is otherwise very similar in expression of spiral sculpture, form of the anterior columella and fasciole, and overall form. Woodring stated that the "strength of late axial ribs on the type of *C. inornatus* is about midway between the extremes shown by *C. ectyphus*." He added, however, that the actual range of variation in *C. inornatus* is unknown.

Calophos ursus (Olsson)
Plate 11, figure 7

Perunassa (?) *ursa* Olsson, 1964, pp. 156–157, pl. 27, fig. 8.
Calophos ursus (Olsson). Woodring, 1964, p. 262.

Occurrence.—Ecuador, Angostura Formation.

Range.—Middle Miocene.

Type locality.—Cueva de Angostura, Río Santiago, Ecuador.

Material examined.—Holotype, USNM 644014; Paratype, USNM 644015; non-type material from USGS loc. 23491 (Mompiche–Potete, Ecuador), USGS loc. 23487 (Cueva de Angostura, Ecuador), and USGS loc. 23490 (Sua, Ecuador) [total: 11 specimens].

Remarks.—Woodring (1964, p. 263) stated that *Calophos* could be separated from *Perunassa* Olsson by the type species of the latter ["*P. zorritensis*" (Nelson, 1870)] being "more inflated than *Calophos*" with "a channeled or shouldered sutural area and the interior of the outer lip [having] weak elongate narrow ridges." *P.* (?) *ursa*, however, is extraordinarily similar, both in overall shape and specific aspects of shell morphology, to *Calophos ectyphus* Woodring, 1964. Both show spiral grooves becoming obsolete in the middle of the whorls, a striated interior of the outer apertural lip, faint axial ribs on the body whorl, and a pronounced basal fold on the columella.

Calophos bombax (Olsson)
Plate 11, figure 6

Perunassa bombax Olsson, 1964, p. 157, pl. 28, fig. 10.
Calophos bombax (Olsson). Woodring, 1964, p. 262.

Occurrence.—Ecuador, Borbon Formation.

Range.—Upper Miocene–lower Pliocene.

Type locality.—Barro Colorado, Río Santiago, Ecuador.

Material examined.—Holotype, USNM 644013.

Remarks.—Details are less easily described on *P. bombax* as the outer shell layer on much of the holotype specimen is broken away. In general outline, it is narrower and more elongate than *C. ectyphus* Woodring, 1964. A terminal columellar fold is present, but is less pronounced than in either *P.* (?) *ursa* Olsson, 1964 or *C. ectyphus* Woodring, 1964. Given the range of variation present in the taxa originally included by Woodring in *Calophos*, however, it is difficult to see how *Perunassa* (?) *ursa* and *P. bombax* can be separated from it at the generic level.

Calophos plicatilis (Böse)
Plate 12, figures 13–15

Cominella plicatilis Böse, 1906, p. 39, pl. 5, figs. 22–24.
non Dorsanum ? plicatilum (Böse). Cooke and Mossom, 1929, p. 139, pl. 16, fig. 3; *nec* Mansfield, 1930, p. 73, pl. 17, fig. 3; *nec* Cooke, 1945, p. 184, figs. 22–23.
non Dorsanum ? plicatile (Böse). Dubar, 1962, p. 43; *nec* Olsson and Petit, 1964, p. 552, pl. 79, fig. 6.
Calophos plicatilis (Böse). Woodring, 1964, p. 262.

Occurrence.—Mexico, horizon unknown.

Range.—Middle Miocene?

Type locality.—Near Tuxtepec, Oaxaca, Mexico.

Material examined.—None.

Types.—Unknown.

Remarks.—Böse gave the heights of two specimens of this species as 29.5 and 23 mm. He stated that the protoconch consists of three whorls with a rounded nucleus.

Böse's illustrations and descriptions make assessment of the affinities of *plicatilis* difficult. It appears to show only slight development of a terminal columellar fold, and little or no development of callus on the lower lip of the aperture. It differs most notably from most other species assigned to *Calophos* in the persistence of spiral sculpture across the entire adult body whorl, rather than becoming obsolete in the middle. As noted by Böse, in this feature it most closely resembles *C. golfoyaquensis* (Maury, 1917), but is larger and the spiral cords are not as sharp.

Calophos wilsoni, new species
Plate 11, figure 14; Plate 12, figures 11, 12

Dorsanum ? plicatilum (Böse). Cooke and Mossom, 1929, p. 139, pl. 16, fig. 3; Mansfield, 1930, p. 73, pl. 17, fig. 3; Cooke, 1945, p. 184, figs. 22–23.

Dorsanum ? plicatile (Böse). Tucker and Wilson, 1932a, p. 14, pl. 5, fig. 7; Tucker and Wilson, 1932b, p. 357; Dubar, 1962, p. 43: Olsson and Petit, 1964, p. 552, pl. 79, fig. 6.

Calophos, n. sp. Woodring, 1964, p. 262 (note 4).

cf. *Dorsanum plicatilum* (Böse, 1906). Campbell, 1974, p. 79, pl. 2, fig. 7.

Etymology of name.—Named in honor of Druid Wilson of the U. S. Geological Survey.

Diagnosis.—Medium to large *Calophos* with relatively high spire, rounded whorl profiles, and short columella. Axial sculpture very faint; spiral sculpture often obsolete over middle of body whorl. Columella separated from body whorl by unique combination of ridge and fold.

Description.—Moderate to very large for genus. Relative spire height comparable to most congeneric species, never exceeding approximately one-third total height. Protoconch consists of 1¼–1½ rounded, unsculptured whorls. Boundary with teleoconch sharp and marked by initiation of clear axial and spiral ribbing. Axial sculpture on some specimens persists on spire whorls, on others quickly becomes obsolete. Observed teleoconch whorls seven to nine. Whorls rounded in profile and somewhat inflated. Sutures relatively deeply incised. Sculpture consists of numerous flat, evenly spaced ribs separated by shallow grooves. Ribs often become faint to obsolete over middle of body whorl, often only faint grooves persisting, or may persist undiminished. Axial sculpture present on body whorl usually only as faint, widely spaced ribs ending adapically as faint nodes slightly below suture and forming very weak shouldering of the body whorl. Aperture broadly lanceolate, approximately one-half total height. Posterior end shows slight notching. Inside of outer lip bears faint to moderate spiral ribs. Outer lip varies in thickness from thin but sturdy to quite thick. Parietal callus weak or absent. Columella relatively short; separated from body whorl by a distinct channel or crease, adapical to a strong spiral cord. Remainder of columella bears five to seven evenly spaced spiral ribs, and ends in a distinct terminal fold. Anterior canal short and relatively wide.

Measurements (total height in mm).—Holotype, MCZ(IP) 29351, 36.0; Hypotype, (Olsson and Petit, 1964, pl. 79, fig. 6), 48.9.

Occurrence.—Florida, Sarasota and Charlotte counties, southwest to Dade County, "Pinecrest Formation" (type); Lee County, Jackson Bluff Formation (Mansfield, 1930); (?) South Carolina, Sumter County, Duplin Formation (Campbell, 1974).

Range.—Lower–upper Pliocene.

Type locality.—APAC Florida Pit, northern Sarasota County, Florida, at junction of Interstate Highway 75 and Fruitville Road ("Pinecrest Formation").

Types.—Holotype, MCZ(IP) 29351; Paratype, MCZ(IP) 29350.

Other material examined.—USNM stratigraphic collection: from USGS locs. 22298, 21907, Acline, Charlotte County, Florida; unnumbered specimens in the paleontological collections of the Department of Geology, University of South Florida, Tampa [total: 75 specimens].

Remarks.—This, the only North American representative of *Calophos*, most closely resembles *C. plicatilis* (Böse), but is larger, and has greater variability in the expression of axial and especially spiral sculpture over the body whorl. Spiral grooves may persist uniformly over the body whorl surface (as in the specimens figured by Olsson and Petit, 1964, pl. 79, fig. 6, and by Campbell, 1974), or become obsolete over this region (as in the holotype) in typical *Calophos* fashion. It closely resembles *C. mixteca* (Perrilliat Montoya, 1963), differing in being larger, relatively wider and having a relatively shorter columella. It is similar to *C. ectyphus* Woodring, 1964, but is larger and more elongate and has a somewhat thinner outer lip. *C. wilsoni* is characterized by a combination of features including short columella with a distinctive ridge-and-fold separating it from the body whorl, relatively high spire, rounded whorl shape with very faint to obsolete axial sculpture, and relatively large size.

No specimens from Jackson Bluff, Lee County, have

been examined, and the only source of information on this occurrence is Mansfield (1930). Olsson and Petit (1964, p. 552) stated that this form is "fairly common at Acline, but rare at other Pinecrest localities." Their figured specimen came from a canal in Dade County. I have also examined specimens referable to *C. wilsoni* collected by E. J. Petuch at the "Bird Road Site" in Miami (see Petuch, 1986) from beds apparently equivalent to the "Pinecrest" beds at Sarasota.

Among the many molluscan species they discuss, Olsson and Petit (1964, p. 517) single out this gastropod as being of particular interest, presumably because it so strongly indicates affinities with Caribbean and Central and South American faunas.

Although the stratigraphic relations and nomenclatural status of the "Pinecrest" and the associated Caloosahatchee Formation remain unresolved (see Missimer, 1984, and Stanley, 1986, for summaries), a Pliocene date for the "Pinecrest" is well supported (*e.g.*, Akers, 1974).

Calophos baranoanus (Anderson)
Plate 11, figure 16

Phos baranoanus Anderson, 1929, p. 137, pl. 16, figs. 4, 5.
Gordanops baranoanus (Anderson). Olsson, 1964, p. 162, pl. 20, fig. 1.
Calophos baranoanus (Anderson). Woodring, 1964, p. 262.

Occurrence.—Colombia, Venezuela, Tuberá Group; Costa Rica (?), Moctezuma Formation.

Range.—Middle–upper (?) Miocene.

Type locality.—North slope of Tuberá Mountain, near Cibarco, northeastern Colombia (CAS loc. 325-A).

Material examined.—Holotype, CAS 4657; Paratype, CAS 4657-A (Plott's Well, SW of Baranoa, Colombia); Hypotype, (Olsson, 1964), USNM 347228 (Cubagua Is., Venezuela); non-type material, from USGS loc. 8101 (Baranoa–Sabana Larga area, Atlántico, Colombia), USGS loc. 11344 (Tuberá, Colombia), USGS loc. 24980 (near Punta Mala, Guanacaste Province, Costa Rica) [total: 11 specimens].

Remarks.—This species differs from other species assignable to *Calophos* in: (1) the development of a marked posterior sinus or canal, a feature incipient but not conspicuous in *C. ectyphus* Woodring, 1964; and (2) greater development of striation on the interior of the outer apertural lip. Anderson's type specimens show ridges lining the aperture from the posterior to the anterior canals. Axial sculpture is much reduced or absent, and the shell surface is marked by moderate to fine spiral ridges and grooves that are obsolete over the middle of the body whorl.

Calophos (?) **esmereldensis** (Olsson)
Plate 11, figure 15

Gordanops esmereldensis Olsson, 1964, p. 162, pl. 20, figs. 2, 2a.

Occurrence.—Ecuador, Esmeraldas Formation; Venezuela, horizon unknown.

Range.—Upper Miocene or lower Pliocene (?).

Type locality.—Punta Gorda, Ecuador.

Material examined.—Holotype, USNM 644203; Paratypes, USNM 644204, 645275; non-type material, from UCMP loc. S-122 (Nueva Esparta, Venezuela) [total: 26 specimens].

Remarks.—Olsson noted the similarity of this species to *C. baranoanus* (Anderson, 1929), particularly in the presence of a marked posterior canal, which in *esmereldensis* is usually enlarged and lengthened. The posterior canal is variable, however, often being little more developed than shown in *baranoanus*. This is the largest form potentially assignable to *Calophos*, the largest specimens exceeding 45 mm total height and 25 mm diameter. It is also the least sculptured; the surface is almost totally smooth, bearing only fine spiral ridges and grooves. The anterior apertural lip flares markedly, and apertural striae are usually lacking or very faint. The anterior columella is similar to that of all other *Calophos* species.

Calophos esmereldensis differs in many respects from the type species of the genus. It appears to represent the extreme expression of several morphological tendencies evident in other *Calophos* species, however, such as reduction of external and internal sculpture, inflation of the body whorl, and development of a posterior notch and canal. It is clearly closely related to these species and is reasonably included in the genus.

Calophos rohri (Rutsch)
Plate 11, figures 8, 17

Phos (?) *rohri* Rutsch, 1942, pp. 150–151, pl. 7, figs. 5, 6.
Calophos rohri (Rutsch). Woodring, 1964, p. 262; Jung, 1969, pp. 514–515, pl. 54, figs. 7–10.

Occurrence.—Trinidad, Savaneta Glauconitic Sandstone Member, Melajo Clay Member, Springvale Formation.

Range.—Upper Miocene–lower Pliocene.

Type locality.—Brechin Castle Estate, Trinidad.

Material examined.—Holotype, NHMB H6187; Hypotypes, NHMB H15215, H15216; non-type material, NHMB H15211, H15214 (Melajo River, Trinidad) [total: five specimens].

Remarks.—Rutsch's holotype is apparently a juvenile, being shorter and relatively more elongate than the other figured specimens, with its last whorl still uniformly covered with spiral grooves. In their relatively inflated body whorls, obsolescence of spiral

sculpture over the middle of the body whorl, and reduced axial sculpture, adult specimens most closely resemble *C. baranoanus* (Anderson, 1929), differing mainly in having a somewhat higher spire, less convex early whorls, and in being generally less robust. The parietal callus is very faint to almost absent. Apertural striae are present only as very faint and widely spaced ridges. Axial sculpture is noticeable on early teleoconch whorls as very fine costae. Jung (1969) states that *C. rohri* shows a "slightly ascending suture near the outer lip", a feature more strongly developed in *C. baranoanus* and *C. esmereldensis*, but I have not observed this feature in the specimens I have examined.

Calophos mixteca (Perrilliat Montoya)
Plate 11, figure 18

Chrysodomus mixteca Perrilliat Montoya, 1963, pp. 21–22, pl. 4, figs. 16, 17.
Calophos mixteca (Perrilliat Montoya). Jung, 1969, pp. 514–515.

Occurrence.—Mexico, Agueguexquite Formation.
Range.—Middle Miocene.
Type locality.—Cuenca Salina, Tehuantepec, Mexico.
Type.—Holotype, G-IGM 1112.
Material examined.—None.
Remarks.—This form bears strong resemblances to other species assigned to *Calophos*. The whorls are similarly inflated and sculptured with closely spaced spiral grooves. These grooves become less pronounced or obsolete in the middle of the body whorl. The columella appears to bear at least something of a terminal fold, although this is not so pronounced as in other species. The outer lip is thin and marked on the inside by incipient spiral ridges.

Perrilliat Montoya suggested that *mixteca* resembles *Chrysodomus parbrazana* Harris, 1895a from Lower Claiborne Group sediments in Texas. The drawing of this form presented by Harris does bear some resemblance to *mixteca*, especially in its very rounded body whorl and simple columella. Photographs of specimens assignable to this or a closely related form presented by Palmer (1937, pl. 38), however, suggest that Harris' drawing may be unreliable in these respects. Palmer and Brann (1966, p. 774) refer *parbrazana* to *Mitrella bucciniformis* (Heilprin, 1879), and this seems a more reasonable assignment.

Calophos golfoyaquensis (Maury)
Plate 11, figure 13

Tritia golfoyaquensis Maury, 1917, p. 92, pl. 15, figs. 24, 25.
Calophos golfoyaquensis (Maury). Woodring, 1964, p. 262.
Nassarius golfoyaquensis (Maury). Cernohorsky, 1984, p. 42.

Occurrence.—Dominican Republic, Cercado de Mao.
Range.—Miocene.
Type locality.—Bluff 3, Cercado de Mao, Dominican Republic.
Material examined.—Syntypes, PRI 28740, 28741.
Remarks.—This species is the smallest of the taxa assignable to *Calophos*, the larger of the two syntypes measuring less than 18 mm in total height. This form appears to most closely resemble *plicatilis* in its overall form, acute, somewhat attenuated spire, relatively inflated and rounded body whorl, absence of axial sculpture, and especially in the dominance of spiral ribbing over the entire body whorl.

Calophos tropicalis (Dall and Ochsner)
Plate 11, figure 11

Alectrion tropicalis Dall and Ochsner, 1928, p. 109, pl. 2, fig. 9.
Nassarius tropicalis (Dall and Ochsner). Cernohorsky, 1984, p. 38.

Occurrence.—Known only from the type locality.
Type locality.—Galapagos Islands, Isla Baltra, "upper horizon . . . probably Pliocene" (Dall and Ochsner); see discussion of age below (p. 78).
Material examined.—Holotype, CAS 2925.
Remarks.—(see below, under *Calophos oldroydae*).

Calophos oldroydae (Dall and Ochsner)
Plate 11, figure 10

Alectrion oldroydae Dall and Ochsner, 1928, p. 110, pl. 2, fig. 10, pl. 6, fig. 8.
Nassarius oldroydae (Dall and Ochsner). Cernohorsky, 1984, p. 38.

Occurrence.—Known only from the type locality.
Type locality.—Galapagos Islands, Isla Santa Cruz.
Material examined.—Holotype, CAS 2926.
Remarks.—These two Galapagos species, *tropicalis* and *oldroydae*, are the only Pacific forms assignable to *Calophos*. The history of their classification is of some interest. The genus *Alectrion* Montfort, 1810 was placed in its own family, the Alectrionidae, by many earlier workers (*e.g.*, Clark and Arnold, 1923; Dall and Ochsner, 1928; Vokes, 1939). More recently it has usually been placed in Nassariidae, frequently as a synonym (*e.g.*, Keen, 1971) or subgenus (Cernohorsky, 1984) of *Nassarius* Duméril, 1806. In 1856, Conrad described the genus *Schizopyga* from material from the Pliocene of California. The type specimen of the type species, *S. californiana*, is apparently lost, but based on Conrad's published figure and examination of further material, Addicott (1965b) suggests that the species belongs in *Nassarius*. In 1928, Dall and Ochsner described *Alectrion tropicalis* and *A. oldroydae* from fossiliferous deposits on the Galapagos Islands, but stated that these species appeared to belong "to the group so well represented in the California Pliocene and recent faunas and called by Conrad *Schizopyga*" (Dall and Ochsner, 1928, p. 109). Cernohorsky (1984, p. 32) considers *Schizopyga* to be a synonym of *Caesia* Adams and

Adams, 1853, which he considers a subgenus of *Nassarius*, represented by living species on the Pacific coast of America.

Dall and Ochsner suggested that *oldroydae* might be allied to *Alectrion perpinguis* Hinds, 1844 and *Alectrion mendica* (Gould, 1850), both of which have lately been referred to *Nassarius* (Abbott, 1974, pp. 224–225; Cernohorsky, 1984, p. 35). *A. perpinguis* is, in fact, the type species for the subgenus *Caesia* (Cernohorsky, 1984). Cernohorsky places *tropicalis* and *oldroydae* in *Nassarius* without discussion (Cernohorsky, 1984, p. 38).

The two Galapagos forms bear considerable resemblance to the species described above in the genus *Calophos*. The spire comprises one-half to one-third the total shell height; there is slight shouldering of the whorls, which are rounded and somewhat inflated; axial sculpture is lacking on later whorls. Spiral sculpture consists of closely spaced grooves, which become faint over the middle of the body whorls. Both forms show terminal columellar folds.

The type specimens are apparently the only known representatives of these taxa. No further material was obtained by either the *Velero III* Expedition in 1931–1932 (Hertlein and Strong, 1939; Hertlein, 1972) or the 1982 expedition organized by Pitt (Pitt, written commun., 1985; results of this expedition have been summarized in Lipps and Hickman, 1982; Pitt and James, 1983; James, 1984; Hickman and Lipps, 1985). From such a small sample it is, of course, impossible to gauge ranges of variation, and the two described species may, in fact, be synonymous (Pitt, written commun., 1985).

The Galapagos fossils more closely resemble species assignable to *Calophos* than they do any living nassarine species. They are, first of all, somewhat larger than most nassariines: *Nassarius perpinguis* ranges from 20 to 25 mm total height, *N. mendicus* approximately 12 to 20 mm (Abbott, 1974) (although *N. fossatus* (Gould, 1850) reaches 50 mm [Nesbitt, written commun., 1987]), while both Galapagos species exceed 30 mm total height. Gross shell morphology is also different; the body whorl and aperture are relatively larger than is typical for most species of *Nassarius*. External sculpture consists largely of spiral ridges; the shell is thinner and more delicate; the outer lip is simple and thin, all in contrast to the characteristic pattern for most species of *Nassarius* (see, *e.g.*, Pl. 1, figs. 1, 2).

On the basis of their size, general form, and sculpture pattern, it is reasonable to assign these two species to the genus *Calophos* Woodring, 1964. Acceptance of this suggestion would probably make them the youngest representatives of *Calophos*. It also implies that they dispersed from the Caribbean region to the Galapagos, and survived there while the other species of the genus became extinct elsewhere.

Dall and Ochsner (1928) and Hertlein (1972) proposed a Pliocene age for the fossiliferous deposits on Isla Baltra (Seymour Island) and Isla Santa Cruz (Indefatigable Island). Based on a more detailed investigation of the stratigraphy and paleontology of these beds, Hickman and Lipps (1985) have suggested an age of between 1.6 and 2.47 ma (late Pliocene), making them among the oldest known fossiliferous sediments on the Galapagos. Biogeographic affinities between the Galapagos fossil fauna and species in the Caribbean are considered by most authors to be unlikely but still possible (Vermeij, 1978, pp. 258–266; James, 1984). The Panamanian isthmus appears to have closed at or around three million years ago, effectively preventing marine faunal interchange between the Pacific and the Caribbean after that time (Keigwin, 1978). The Galapagos seem to have existed as subaerial islands since at least three million years ago (Cox, 1983; Simkin, 1984a; Simkin, 1984b; Hickman and Lipps, 1985). These dates may have allowed for a "window" during which Caribbean species could have reached the Galapagos (James, 1984, p. 80).

Keen (1976) noted that many mollusks of Caribbean origin persisted on the Pacific side of the isthmus as far north as California into the Plio-Pleistocene, after their ancestors and relatives had become extinct on the Caribbean side. The Galapagos species of *Calophos* may represent additional examples of taxa that survived in this eastern Pacific refugium.

Calophos ? zorritensis (Nelson)
Plate 12, figures 8, 9

Argobuccinum zorritense Nelson, 1870, p. 196, pl. 7, figs. 1, 2.
Nassa zorritensis (Nelson). Spieker, 1922, p. 48, pl. 2, figs. 1, 2.
Buccinanops (*Perunassa*) *zorritensis* (Nelson). Olsson, 1932, pp. 168–170, pl. 20, figs. 1–5.
Perunassa zorritensis (Nelson). Cernohorsky, 1984, p. 27.

Occurrence.—Peru, Tumbez Formation.

Range.—Upper Miocene.

Type locality.—Trucillal, Peru.

Material examined.—Figured syntypes, YPM 504; unfigured syntypes, YPM 598, 599, 600, 2126–2136 [total: 15 specimens].

Other types.—Figured syntype, YPM 597 apparently lost [*fide* White, written commun., 1986].

Remarks.—In his discussion of this species, Spieker (1922) noted that it was "difficult to place generically," and stated that he was assigning it only tentatively to the genus *Nassa* Lamarck, 1799. Spieker suggested that *zorritensis* most closely resembled *Nassa veneris* Faujas de Saint-Fond, 1817, observing further that the latter form probably did not belong to the genus *Dorsanum*

Gray, 1847. He suggested that the two species "are of a subgroup yet to be designated . . ." (Spieker, 1922, p. 49) (see pp. 86, 108).

Olsson (1932) placed *zorritensis* in a new subgenus *Perunassa* in the genus *Buccinanops* d'Orbigny, 1841, describing *Perunassa* as follows:

> Shell rather large, with an elevated spire and larger body whorl; nucleus unknown; nepionic whorls convex, ornamented with spirals, the penultimate and last whorl becoming narrowly shouldered and ribbed, the ribs being located principally on the shoulder angle; the spirals tend to disappear on the later turns or persist principally on the shoulder or on the base; anterior canal stout, twisted and with a sharp fold at its lower end and a wide, deep siphonal sinus; a strong nassoid keel emerging from the middle of the columella encircles the beak above the siphonal fasciole; outer lip slightly oblique. (Olsson, 1932, p. 168)

Comparing it with the living Patagonian species *Buccinanops paytense* (Kiener, 1834), *B. cochlidium* (Dillwyn, 1817), and *B. moniliferum* (Kiener, 1834), Olsson concluded that, although *zorritensis* was "clearly not a true *Buccinanops* . . . it seems more nearly related to that genus than any other established group." *Perunassa* differed from *Buccinanops* s. s., said Olsson, in the greater degree of sculpturing on the whorls.

In describing two new species from the Miocene and Pliocene of Ecuador, Olsson (1964) elevated *Perunassa* to genus level and placed it, without explanation, in Buccinidae. In his revised description of the genus, Olsson once again noted, however, that the columella "is stout, straight, with a large plait at its end, encircled externally by a wide siphonal fasciole bordered by a nassoid keel" (Olsson, 1964, p. 156). Although Cernohorsky (1984, p. 27) has recently supported the placement of *Perunassa* in Buccinidae, Olsson's redescription and an examination of his specimens seem to ally it more closely with Nassariidae.

The species *zorritensis* seems to be distinct from the three other species assigned to *Perunassa* in its lack of spiral sculpture, its conspicuously shouldered profile and the form of its axial sculpture, which is comprised of a series of moderately spaced rounded knobs along the whorl shoulders. Axial ribs as such are not present on the body whorl. The anterior end of the columella bears a simple but a very profound terminal fold.

This species most closely resembles species assignable to *Calophos* Woodring, 1964, especially *C. tropicalis* (Dall and Ochsner, 1928), but differs from most of these species in its squarish whorl profile, lack of apertural striae, and knobby axial sculpture. The terminal columellar fold strongly suggests that it is nassariid, but its larger size and lack of pronounced spiral sculpture over the body whorl distinguish it from species of Nassariinae. It does not especially resemble either fossil or living species of *Buccinanops* (see p. 20). I assign *zorritensis* to *Calophos* with some reservation. It is possible that this species is most closely related to South American (or the Galapagos) species of *Calophos*, but represents a separate lineage deserving generic or subgeneric ranking and retention of the name *Perunassa* Olsson, 1932. Its stratigraphic and geographic position, as well as some aspects of its morphology, lend some support to this interpretation.

Genus **PERUNASSA** Olsson, 1932

Type species.—*Argobuccinum zorritense* Nelson, 1870.

"**Perunassa**" **ecuadorensis** (Pilsbry and Olsson)

Plate 12, figure 1

Nassa (*Perunassa*) *ecuadorensis* Pilsbry and Olsson, 1941, pp. 31–32, pl. 4, figs. 2, 8, 11.
Perunassa ecuadorensis (Pilsbry and Olsson). Olsson, 1964, p. 156.
Nassarius eguadorianus [*sic*] (Pilsbry and Olsson). Cernohorsky, 1984, p. 37.

Occurrence.—Ecuador, Punta Blanca beds, Canoa Formation, Jama Formation.

Range.—Lower Pliocene.

Type locality.—Punta Blanca, Ecuador.

Material examined.—Three syntypes, ANSP 13651; Apparent topotypes, ANSP 15256 [total: 19 specimens].

Remarks.—Although assigned to *Perunassa* by Olsson, this species does not agree with either the type species, *zorritensis* (Nelson, 1870) [here tentatively assigned to *Calophos*] or the other two species, *Calophos ursus* (Olsson, 1964) and *C. bombax* (Olsson, 1964). Olsson (1964) stated that the nuclear whorls of *ursa* were similar to those of *ecuadorensis*, which Pilsbry and Olsson described as "very small". Except in overall proportions and form, *ecuadorensis* differs from all other species in the *Bullia* group in almost all other shell characters. Its axial sculpture is conspicuous, the axial ribs being more pronounced, narrow, numerous, and closely spaced than those in any species of *Calophos*. Neither spiral nor axial sculpture becomes obsolete in the middle of the body whorl. As it does not agree with the type species of *Perunassa*, this species should not be placed in that genus. It most resembles species of "*Phos*-like" genera such as *Cymatophos* Pilsbry and Olsson, 1941, and *Metaphos* Olsson, 1964, differing primarily in having a relatively slightly shorter spire. It is probably more closely related to these taxa than to members of the *Bullia* group.

CENOZOIC OF SOUTHERN SOUTH AMERICA AND ANTARCTICA

Tertiary marine sediments of southeasternmost South America contain species closely related to species

living off the Patagonian coasts today. These forms occur in deposits which were last studied paleontologically by American, Argentinian, and Brazilian workers around the turn of the century, and are only now beginning to be reanalyzed [see Zinsmeister (1981) for an account of the history of paleontological investigation in this region].

Ihering (1899, 1907) summarized the occurrence of Tertiary molluscan fossils in Patagonia. He reported Recent species of "*Bullia*" from the uppermost horizons of the Patagonian Cenozoic section (Table 10). Subsequent reassessment of the ages of these and other horizons discussed by Ihering (Table 11) has not altered his claim that no representative of the *Bullia* group appears in the fossil record of this area until the Pliocene (Ihering, 1907, pp. 510–511) [see also Pilsbry, 1897a, and Feruglio, 1933, 1949–1950 for fossil occurrences of these species in Patagonia]. Although he described a new subspecies from the "Auraucanian" horizon (*B. gradata pampeana* Ihering, 1907), Ihering did not identify any extinct species of the group. Subsequently, however, at least one and possibly two valid forms have been recognized as assignable to *Buccinanops*.

Table 10.—Stratigraphic distribution of fossil species of *Buccinanops* in Patagonia given by Ihering (1907) [A] and Carcelles and Parodiz (1939) [B]. Recent reinterpretation of the ages of these stratigraphic horizons shown in Table 11.

horizon	*locality*	*species*
A		
Araucanienne	Puerto Piramides	*globulosum*
Pampienne, Post Pampienne	Puerto Militaire	*globulosum* *cochlidium* *gradata pampeana* *deformis*
	Rio de La Plata	*deformis* *globulosum*
Post-Tertiares	Punta Carretas Montevideo	deformis globulosum gradatum
B		
Post Pampean	Puerto Belgrano	*moniliferum* *deformis* *globulosum*
Quaternary	Punta Carretas	*globulosum* *deformis*
	Porto Madryn	*cochlidium*
	Riacho del Ingles	*cochlidium*
	Bahia San Blas	*cochlidium*
Pampean	Porto Belgrano	*uruguayensis* *deformis*
Araucanienne	Sierra Laziar	*globulosum*

Genus **BULLIA** Gray *in* Griffith and Pidgeon, 1834

Type species.—*Bullia semiplicata* Gray, 1834.

Subgenus **BUCCINANOPS** d'Orbigny, 1841

Type species.—*Buccinum globulosum* Kiener, 1834.

Bullia (Buccinanops) fuegina
(Steinmann and Wilckens)
Plate 12, figures 6, 7

Nassa fuegina Steinmann and Wilckens, 1908, pp. 65–66, pl. 7, figs. 1a, b.

Cominella wilckensis Ihering, 1909, p. 32 [*fide* Malumian, Camacho, and Gorroño, 1978, p. 280].

"*Nassa*" *fueguina* [*sic*] Steinmann and Wilckens. Malumian, Camacho, and Gorroño, 1978, pp. 208–282, pl. 2, fig. 3.

Occurrence.—Tierra del Fuego, Isla Grande; Antarctica, Seymour Island.

Range.—Lower Miocene.

Material examined.—MCZ(IP) 29289 (Isla Grande, Tierra del Fuego) [total: two specimens].

Types.—Unknown.

Remarks.—[see below, under *Bullia* (*Buccinanops*) *nordenskjoldi*].

Bullia (Buccinanops) nordenskjoldi
(Steinmann and Wilckens)
Plate 12, figure 5

Nassa Nordenskjoldi Steinmann and Wilckens, 1908, pp. 75–76, pl. 7, figs. 2a, b.

Bullia [sp.] Wilckens, 1906, p. 176 [*fide* Steinmann and Wilckens, 1908, p. 66].

Occurrence.—Tierra del Fuego.

Range.—Lower Miocene.

Material examined.—None.

Types.—Unknown.

Remarks.—*B.* (*B.*) *fuegina* and *B.* (*B.*) *nordenskjoldi* are very similar to Recent species of *Buccinanops* from Patagonia. Both *nordenskjoldi* and *fuegina* have relatively short spires, relatively inflated body whorls, well-developed terminal columellar folds, and lack axial sculpture. In these respects they especially resemble living species such as *Buccinanops paytense* (Kiener, 1834) and *B. globulosum* (Kiener, 1834). They differ

Table 11.—Revised chronostratigraphic classification for the Tertiary of Patagonia (after Zinsmeister, written commun., 1985).

horizon	*Ihering's (1907) age*	*revised age*
Postpampian	Quaternary	Holocene
Pampian	upper Pliocene	Plio-Pleistocene
Araucanian	lower Pliocene	Plio-Pleistocene
Entrerian	Miocene	middle–upper Miocene
Magellanian	Oligocene	Miocene
Superpatagonian	upper Eocene	Eocene
Patagonian	Eocene	Eocene

primarily in having faint to moderate spiral grooves covering most of the whorl surfaces; this appears to be less pronounced in *nordenskjoldi* than in *fuegina*. On the basis of these resemblances to these Recent species, I have assigned them to *Buccinanops*.

Steinmann and Wilckens observed that *nordenskjoldi* and *fuegina* differ in size, shape, and external sculpture. In a similar number of whorls, *nordenskjoldi* is more than twice as large as *fuegina*. The spire of *nordenskjoldi* is more flattened and the last whorl more inflated. These two species also appear to differ in the development of the parietal callus, which is relatively thick in *nordenskjoldi* but barely present in *fuegina*, and the shape of the aperture, which is much wider in *nordenskjoldi*. It is possible that *fuegina* represents the juvenile form of *nordenskjoldi*; the weaker development of the callus and the more prominent spiral lirae on the former supports this interpretation.

Both *nordenskjoldi* and *fuegina* are very common on Isla Grande, Tierra del Fuego (Zinsmeister, written commun., 1985). The sediments in which they occur were considered to be of Early Tertiary age by Steinmann and Wilckens, and Eocene or early Oligocene by Camacho (1974) and Malumian, Camacho, and Gorroño (1978). Radiometric age determinations on tuffs from at least one locality in Tierra del Fuego, however, seem to suggest an early Miocene age (Zinsmeister, written commun., 1985).

Cernohorsky (1984, p. 23) believes that *nordenskjoldi* is a species of *Buccinanops*, but he suggests that *fuegina* actually belongs to the buccinid genus *Chlanidota* Martens, 1872. Comparison of *fuegina* with the figure of the type species of *Chlanidota, C. vestita* Martens *in* Wenz, 1943 [p. 1201, fig. 3419], however, does not support this conclusion. Although *C. vestita* is generally similar in overall form to both *fuegina* and *nordenskjoldi*, it appears to lack the terminal columellar fold clearly present in *fuegina*.

Although Malumian, Camacho, and Gorroño (1978) tentatively place *fuegina* in the genus *Nassa* Lamarck, 1799, they suggest that it in fact belongs to an undescribed buccinid genus. These authors mistakenly state that Ihering (1909) suggested that *fuegina* be placed in the genus (or subgenus) *Austrocominella* Ihering, 1907. Their reasons for disagreeing with this are valid enough, but Ihering (1909) was, in fact, discussing *Cominella* (*Austrocominella*) *fuegensis* (see discussion immediately below).

A number of undescribed taxa of gastropods from Paleogene sediments of Seymour Island, Antarctica are similar to these Fuegian species. In 1906, Wilckens included specimens he said could be assigned to *Bullia* in a brief discussion of invertebrate faunas from this area. Steinmann and Wilckens (1908, p. 66) indicated in their original description of *Nassa fuegina* that this was the form mentioned earlier by Wilckens. The molluscan faunas of Seymour Island appear to be of late Eocene to early Oligocene age (Zinsmeister and Camacho, 1980; Zinsmeister, 1982, 1984). There are many undescribed bucciniform species from these deposits, some of which resemble South American representatives of the *Bullia* group, and some which are quite different (Zinsmeister, written commun., 1985).

Although at least one species of *Buccinanops* is today found on the West Coast of southern South America, no fossil specimens referable to *Buccinanops* have been reported from anywhere north of Tierra del Fuego on the west coast (see, *e.g.*, Philippi, 1887; Herm, 1969; Fleming, 1972). This suggests that the arrival of *Buccinanops* in this area was a relatively recent event, possibly as late as Holocene.

Genus **AUSTROCOMINELLA** Ihering, 1907

Type species.—*Cominella* (*Austrocominella*) *fuegensis* Ihering, 1907.

Austrocominella fuegensis (Ihering)

Plate 12, figure 10

Cominella (*Austrocominella*) *fuegensis* Ihering, 1907, pp. 343–344, pl. 14, figs. 97a, b.

Cominella obese Philippi var. *fuegina* Steinmann and Wilckens, 1908, p. 60, pl. 6, figs. 3, 4.

Cominella fuegensis Ihering. Ihering, 1909, pp. 31–32.

Austrocominella fueguensis [*sic*] Ihering. Malumian, Camacho, and Gorroño, 1978, pp. 278–280, pl. 2, fig. 1.

Occurrence.—Southern Argentina, Río Tubio Formation; Tierra del Fuego; Chile, Loreto Formation.

Range.—Lower Miocene ?

Material examined.—MCZ(IP) 29290 (Tierra del Fuego) [total: two specimens].

Types.—Museo Nacional, Buenos Aires [*fide* Ihering, 1907, p. 343].

Remarks.—Ihering (1907, p. 190, 344) erected the subgenus *Austrocominella* for species intermediate in form between *Cominella* s. s. and *Ptychosalpinx* Gill, 1867. The genus name *Cominella* has been widely misapplied (see Nuttall and Cooper, 1973) and assignments to it are to be approached with caution. Specimens I have examined (provided by W. J. Zinsmeister) from Tierra del Fuego show a pronounced terminal columellar fold. This species, in fact, bears striking resemblance to species of *Buccinopsis* Conrad, 1857, from the Cretaceous of the southeastern U. S. (see pp. 52, 53). Both forms have closely spaced spiral cords covering all or most of the shell, incipient to pronounced axial ribs or nodes which are most conspicuous on the whorl shoulders, relatively large apertures, elongate, reflexed anterior canals, a relatively complex fasciole, and relatively short spires.

A number of other South American species have been allied with *Austrocominella*, including some from beds identified as Cretaceous (see Table 3b). Finlay

and Marwick (1937) noted similarities between *A. fuegensis* and species of *Zealandiella* Finlay, 1926, from the Tertiary of New Zealand, and suggested that they might be congeneric. The species figured by Finlay and Marwick do not appear to show marked terminal columellar folds, although damage to the columellae and the quality of the illustrations makes judgement difficult. Species of *Zealandiella* range from the Danian to the Pliocene of New Zealand (Wenz, 1941, p. 1165).

With its pronounced terminal columellar fold, *A. fuegensis* might be considered a nassariid by the criteria discussed in this paper. It is tempting to suggest that it represents a form retaining aspects of the ancestral nassariid morphology shown by *Buccinopsis* Conrad, 1857, and surviving in the Southern Hemisphere long after the ancestor disappeared from North America. The possibility that forms from the New Zealand Tertiary may be allied with it only adds interest to this idea. For present purposes, I will speculate no further than this, and leave *Austrocominella* as yet another group of species in need of detailed study.

CENOZOIC OF EUROPE

Genera of Nuttall and Cooper

Nuttall and Cooper (1973) described five new nassariid genera from among more than 30 species of Tertiary neogastropods that had previously been referred to the genus *Cominella* J. E. Gray (*in* M. E. Gray, 1850; see Table 3a). At least four of the five appear to be closely related to the *Bullia* group. My assessment of these genera is based on examination of original plate photographs kindly provided by J. Cooper and C. P. Nuttall of the BM(NH). Complete diagnoses are given in Nuttall and Cooper (1973).

Genus **PSEUDOCOMINELLA** Nuttall and Cooper, 1973

Type species.—*Pseudocominella deserta* (Solander, 1766) [Pl. 15, fig. 2].

Occurrence of the genus.—Middle Eocene (Lutetian) to lower Oligocene of Britain, France, Belgium, Holland, Germany, and the Ukraine.

Remarks.—*Pseudocominella* is the most heavily ornamented of the genera described by Nuttall and Cooper; all species bear pronounced spiral and axial sculpture. The genus cannot be defined by the pattern of sculpture on the early teleoconch, as *P. solanderi* (Cossmann, 1889) [Pl. 15, fig. 3] shows axial costae on its early teleoconch whorls while *P. bullata* (Philippi, 1847) shows only spiral cords on the adapical margin of the early whorls. Also striking is the degree of development of axial sculpture in *P. armata* (Sowerby, 1850) [Pl. 15, fig. 1]. Species of this genus show a terminal columellar fold, and so would seem to be nassariid, but their outward similarity to species in the Melongenidae (*e.g.*, *Busycon* Röding, 1798) is notable. Within Nassariidae they most closely resemble species of the Cretaceous genus *Buccinopsis* Conrad, 1857, especially in their well-developed sculpture, relatively low spire, and relatively elongate anterior canal, although not all species agree with respect to the last two characters.

Nuttall (written commun., 1985) has noted that in the few specimens of *Pseudocominella* with protoconchs sufficiently well-preserved for detailed study, there are indications that development may have been planktotrophic. The condition of most specimens, however, prevents confirmation of this suggestion.

The easternmost occurrence of *Pseudocominella* appears to be that reported by Zelinskaya *et al.* (1968, p.58) from the Eocene of East Germany and the southern Ukraine.

Genus **DESORINASSA** Nuttall and Cooper, 1973

Type species.—*Desorinassa desori* (Deshayes, 1865) [Pl. 15, figs. 4, 5].

Occurrence.—Paleocene (Thanetian) to lower Eocene (Cuisian), Britain and France.

Remarks.—Nuttall and Cooper state that *Desorinassa* is distinguished from *Pseudocominella* Nuttall and Cooper, 1973, "by its curved columella and its weaker sculpture, in particular the almost complete lack of collabral elements." They add that the fasciole resembles that of *Keepingia* Nuttall and Cooper, 1973 and *Thanetinassa* Nuttall and Cooper, 1973. The great resemblance of *Desorinassa* to forms from the Eocene of Alabama, and the differences between the described species with regard to the callus, are discussed on p. 55. The protoconch is known for only one of the two species described by Nuttall and Cooper, *D. desori*, and is described as "worn but appears to have been similar to that of *Pseudocominella*, consisting of about three smooth, naticoid whorls; initially it may have been somewhat flattened" (Nuttall and Cooper, 1973, p. 303). This description is very similar to that of specimens of *Bulliopsis* Conrad, 1862a (p. 46 herein), further supporting a close relationship between these two taxa.

Genus **WHITECLIFFIA** Nuttall and Cooper, 1973

Type species.—*Whitecliffia suturosa* (Nyst, 1836).

Occurrence.—Upper Eocene (Priabonian) to middle Oligocene (Rupelian) of Britain, Holland, Belgium, and Germany.

Remarks.—Although Nuttall and Cooper suggest that this genus arose from *Pseudocominella* Nuttall and Cooper, 1973, it seems to resemble more closely *Desorinassa* Nuttall and Cooper, 1973, in sculpture and overall shell form. Species of the genus resemble species

of *Bulliopsis* from the Alabama Eocene, as well as other fossil species assigned to the *Bullia* group, in the distribution of spiral sculpture over the surface of the last whorl. As in *Pseudocominella*, the pattern of sculpture on the early whorls of the teleoconch is variable, not only between species but also within species. *Whitecliffia suturosa* (Nyst, 1836), as represented by the specimens figured by Nuttall and Cooper, shows no axial sculpture on the early whorls [Pl. 15, fig. 6]. *Whitecliffia tumida* Nuttall and Cooper, 1973, however, includes specimens which show well-developed axial sculpture on early whorls as well as some which show only spiral cords [Pl. 15, fig. 7]. Nuttall (written commun., 1985) reports that both *Whitecliffia* and *Keepingia* Nuttall and Cooper, 1973 "had bulbous apices and could have been either ovoviviparous and/or with encapsulated development."

Genus **COLWELLIA** Nuttall and Cooper, 1973

Type species.—*Colwellia flexuosa* (Edwards, 1866) [Pl. 15, fig. 9].

Occurrence.—Middle Eocene (Auversian) to upper Eocene to Britain, France, and possibly into the Miocene of the West Coast of the U. S.

Remarks.—The morphological relationships of the European and American species possibly assignable to this genus are discussed on pp. 69, 70. Nuttall and Cooper (1973, p. 209) state that *Colwellia* can be distinguished from *Desorinassa* Nuttall and Cooper, 1973, by the form of the subsutural ramp: "In *Desorinassa* the ramp is convex and the collabral sculpture is much stronger on the earlier whorls." They further suggest that *Colwellia* may have arisen from *Desorinassa* and that *D. williamsi* Nuttall and Cooper, 1973 (Paleocene of Britain) and *C. auversiensis* (Deshayes, 1865) (Eocene of France) may form "a link between the two genera."

Genus **KEEPINGIA** Nuttall and Cooper, 1973

Type species.—*Keepingia gossardi* (Nyst, 1836) [Pl. 15, fig. 8].

Occurrence.—Lower Oligocene (Lattorfian) to lower Miocene (Burdigalian) of France, Belgium, Holland, and Germany (and possibly the Rupelian of Pakistan).

Remarks.—Nuttall and Cooper indicate that *Keepingia* is very similar to *Colwellia* Nuttall and Cooper, 1973, differing mainly in the form of the protoconch, which is large and paucispiral, but slightly heterostrophic. Spiral sculpture covers the entire shell. Axial sculpture persists in most species onto the body whorl of adults. A well-developed reflexed siphonal channel is present around the fasciole. Most representatives do not bear any striations on the interior of the apertural lip, although one specimen figured by Nuttall and Cooper appears to show faint denticles. Nuttall and Cooper (1973, p. 209) suggest that *Keepingia* may have arisen from *Colwellia*. *Keepingia* is the only genus discussed by these authors that extends into the Miocene. It is not known from England. If *Cominella annandalei* Vredenburg, 1925, from the upper Oligocene of Pakistan, belongs to *Keepingia*, however, it is the only known pre-Pliocene representative of the *Bullia* group from the Indian Subcontinent (see p. 89).

Genus **THANETINASSA** Nuttall and Cooper, 1973

Type species.—*Thanetinassa bicorona* (Melleville, 1843) [Pl. 15, fig. 10].

Occurrence.—Paleocene (Thanetian) of Britain and France.

Remarks.—*Thanetinassa* strongly resembles several of the species from the Neogene of continental Europe discussed in the following section (pp. 83–86). Nuttall and Cooper have also suggested that it be compared with *Buccitriton* Conrad, 1865a, *Tritiaria* Conrad, 1865a, and *Sagenella* Conrad, 1865b, all from the Paleogene of the southeastern U. S.:

> In all three the fasciole is bounded by a much weaker ridge than in *Thanetinassa*, and the stromboid notch is either weak or absent and is never associated with strong spiral ribs. In *Buccitriton* the columella is short, terminating well above the most anterior part of the shell, which in this case is the outer lip. In *Thanetinassa*, on the other hand, the terminal columellar plait forms the most anterior portion of the shell. In *Tritiaria* the fasciole is much narrower than in *Thanetinassa* and is spirally striate" (Nuttall and Cooper, 1973, p. 213).

Thanetinassa is unique among all taxa discussed here in bearing a strong "stromboid-like" notch at the anterior end of the aperture. Nuttall and Cooper (1973) point out that all species of *Phos* Montfort, 1810 and many species of *Nassarius* Duméril, 1806 show similar notches, and Nuttall (written commun., 1985) believes that *Thanetinassa* belongs to the "*Phos*-group", in Buccinidae s. l.

Problematic Continental Forms

Tertiary sediments of continental Europe contain a great diversity of small- to medium-sized bucciniform gastropods, many of which have, at one time or another, been allied with the *Bullia* group, usually being placed in the genus *Dorsanum* Gray, 1847. My objective in this section is not to attempt the thorough restudy of these taxa that is badly needed, but rather to evaluate in a general way previous proposals of affinity between these species and the *Bullia* group.

The taxonomic treatment of these forms has in a way been somewhat atypical of much of older paleontological and malacological tradition. The tendency in this case has been to describe large numbers of species within existing genera (often variously transmuted as

Table 12a.—Species from the Tertiary of continental Europe previously assigned to the genus *Dorsanum*. Parentheses indicate original description under a different genus.

species	*original author*	*author referring to* Dorsanum
aequistriatum	Dollfus, 1889	Dollfus, 1889
akburunensis	(Andrusov, 1902)	Zelinskaya *et al.*, 1968
angusta	(Hölzl, 1958)	Nuttall and Cooper, 1973
aquense	(Grateloup, 1840)	Peyrot, 1925–1926
armavirensis	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
baccatum	(Basterot, 1825)	Cossmann, 1901b
bosphoranum	(Andrusov, 1902)	Zelinskaya *et al.*, 1968
carabinicum	(Kudrjawzev, 1928)	Zelinskaya *et al.*, 1968
cerithiformis	(Hoernes and Auinger, 1882)	Friedberg, 1928
corbianum	(d'Orbigny, 1845)	Zelinskaya *et al.*, 1968
daveluinum	(d'Orbigny, 1845)	Zelinskaya *et al.*, 1968
dgorlykensis	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
dissitum	(Dubois de Montpereux, 1831)	Zelinskaya *et al.*, 1968
dubium	Peyrot (1925–1926)	Peyrot (1925–1926)
duplicatum	(Sowerby, 1832)	Friedberg, 1911
fraudulentum	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
gradatum	Peyrot, 1925–1926	Peyrot, 1925–1926
grundense	(Hoernes and Auinger, 1882)	Sieber, 1958
haueri	(Hilber, 1879)	Cossmann, 1901b
ignobilis	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
impexum	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
intermedium	Hölzl, 1958	Hölzl, 1958
jacquemarti	(d'Orbigny, 1845)	Zelinskaya *et al.*, 1968
janitor	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
krokosi	(Ossaulenko, 1936)	Zelinskaya *et al.*, 1968
leioconcha	(Andrusov, 1902)	Zelinskaya *et al.*, 1968
lominickii	Friedberg, 1911	Friedberg, 1911
lymnaeformis	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
mirandum	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
multicostatum	(Kudrjawzev, 1928)	Zelinskaya *et al.*, 1968
nasutum	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
nodosocostatum	(Hilber, 1879)	Cossmann, 1901b
omnivagum	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
opinabile	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
orgeevensis	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
plicatum	(Grateloup, 1840)	Peyrot, 1925–1926
pseudogracile	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
ruidum	Peyrot, 1925–1926	Peyrot, 1925–1926
scalaris	(Andrusov, 1902)	Zelinskaya *et al.*, 1968
seminudum	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
semiovalis	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
stavropolensis	(Kudrjawzev, 1928)	Zelinskaya *et al.*, 1968
subpolitum	(d'Orbigny, 1852)	Cossmann, 1901b
superabilie	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
ternodosum	(Hilber, 1879)	Cossmann, 1901b
torpidum	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
triformis	(Kolesnikov, 1932)	Zelinskaya *et al.*, 1968
tscharnozkii	(Kudrjawzev, 1928)	Zelinskaya *et al.*, 1968
veneris	(Faujas de Saint-Fond, 1817)	Cossmann, 1901b

subgenera of each other), rather than to erect new genera, as has often been the case in other groups. That "lumpers" have held sway over "splitters" in this group may indicate something important about variability among species, but one result has surely been to obscure rather than illuminate relationships both among these species and between them and others from elsewhere. The work of Nuttall and Cooper (1973), discussed in the previous section, has contributed to breaking a similar taxonomic logjam that had built up in the genus *Cominella* J. E. Gray *in* M. E. Gray, 1850. No similar recent effort has been made on continental European species commonly placed in *Dorsanum*, and a full understanding of their relationships must await such revision.

Between 50 and 75 named species from the European Tertiary are of interest here (Table 12a; Pl. 13). In general, they all show moderate to well-developed

Table 12b.—Species from the Tertiary of continental Europe previously assigned to the genus *Cyllenina* (by Bellardi, 1882).

ancillariaeformis (Grateloup, 1834)
bicoronata Bellardi, 1882
haueri (Michelotti, 1847)
irregularis Bellardi, 1882
ovulata Bellardi, 1882
paulucciana (d'Ancona *in* Foresti, 1868)
pleurotomoides Bellardi, 1882
recens Bellardi, 1882
sismondi Bellardi, 1882
subumbilicata Bellardi, 1882
terebrina Bellardi, 1882

spiral and axial external sculpture. The anterior portion of the columella and fasciolar region is variable in form, and may offer the most important evidence about relationships. All show some form of terminal columellar fold. At least some forms show a reflexed siphonal channel around the fasciole, bordered on either side by a strong carina. This feature is highly variable, however, for in otherwise identical individuals any trace of such a channel is absent (see Pl. 13, figs. 5–7).

The majority of these shells have a subsutural ramp or sloping shelf, on the lower (*i.e.*, anterior) margin of which are usually developed small nodes, consisting of the posterior extensions of axial ribs which extend anteriorly over the remainder of the body whorl. On the upper (posterior) margin, immediately below the suture, there may be only spiral cords (as in *Nassa veneris* Faujas de Saint-Fond, 1817), but in many forms a series of tubercles develops here (*e.g.*, *Buccinum baccatum* Basterot, 1825; *B. nodosocostatum* Hilber, 1879). Virtually all intermediate stages in this series are displayed. Another common feature is the presence of strong spiral sculpture on the anterior portion of the body whorl, even when it is not present on the middle and upper portions. Denticles or striations are frequently present inside the outer lip of the aperture, but this character is apparently variable within species. Total height in these species ranges from approximately 45 mm to less than 10 mm.

Scanning electron micrographs of protoconchs of three of these problematic European species are shown in Plate 14. All are relatively small [apparent diameters falling within the planktotrophic range; compare with protoconchs of *Dorsanum miran* (Bruguière, 1789), Pl. 6, figs. 5–8]. Boundaries and the protoconch–teleoconch transition are indistinct.

Cossmann's (1901b) treatment of the genus *Dorsanum* was based on the living species *D. politum* (Lamarck, 1822) [= *D. miran* (Bruguière, 1789)]. His study of European fossil material, however, led him to suggest that the genus was not a homogeneous one and that its fossilized morphologic (and taxonomic) diversity was greater than that displayed by its few living species. Cossmann noted that axial costae are present in *D. politum* only on the first whorls of the teleoconch, while in most of the fossil species the costae persist onto later whorls and many species are highly sculptured over the entire shell surface. The only illustrations of *Dorsanum* in Cossmann's "Essais" are of these distinctively sculptured European fossil forms (Cossmann, 1901b, pl. 9, figs. 20–22).

Although Cossman observed that the extreme "nodular" and smooth forms differed more than many genera he had described, he united them within *Dorsanum*, and would not even propose formal subgeneric divisions. A range of intermediate morphologies, he said, joined the nodular and smooth forms and, in any case,

> . . . in examining closely the aperture of the nodular shells, we do not perceive a difference with those of *Dorsanum* [s. s.]; the only reason to separate them is the sculpture, and even it undergoes such gradual transformation that one would be hard pressed to use it to classify certain species. (Cossmann, 1901b, p. 219; translation).

With its primarily spiral sculpture, *Nassa veneris* Faujas de Saint-Fond, 1817 would, Cossmann argued, require its own subdivision, if any were to be recognized at all.

Cossmann thus chose to interpret the living species of *Dorsanum* as representative of only a small portion of the variability expressed in its putative ancestral lineage. Based on little more than their shared buccciniform shape, he grouped a host of European Tertiary taxa in this genus, setting a precedent followed by most European workers ever since (*e.g.*, Peyrot, 1925–1926; Hölzl, 1958; Strausz, 1966; Zelinskaya *et al.*, 1968).

A taxonomic alternative to Cossmann's broad interpretation of *Dorsanum*, however, had already been proposed by Bellardi (1882). Several of the species placed in *Dorsanum* by later authors were originally described by Bellardi under his genus *Cyllenina*. Although Cernohorsky (1984, p. 217) included *Cyllenina* as a subgenus within the living Indo-Pacific nassariid genus *Cyllene* Gray, 1834, elsewhere (Cernohorsky, written commun., 1986) he has suggested that *Cyllenina* is probably not closely related to *Cyllene*, and may be closer to *Desorinassa* Nuttall and Cooper, 1973. Nuttall (written commun., 1985) has suggested that *Cyllenina* may be closer to *Dorsanum* s. s. than to *Cyllene*.

For present purposes it is useful to ask what, if any, characters link these European Tertiary species to members of the *Bullia* group. All of these fossils differ from the living species of *Dorsanum* in showing well-developed axial and spiral sculpture on adult whorls. At least some of these species, however, share with *Dorsanum miran* (Bruguière, 1789) a small multispiral protoconch and a reflexed siphonal channel around the

anterior end of the fasciole, although the latter character is highly variable. This group is referred to as "*Cyllenina*" 2 in the phylogenetic analysis on pp. 104–107. Others seem to resemble the genus *Thanetinassa* Nuttall and Cooper, 1973, in apertural form, relative spire height, and external sculpture. These are referred to as "*Cyllenina*" 1 (see, *e.g.*, *Buccinum duplicatum* Sowerby, 1832 [Pl. 13, fig. 5]; "*Buccinum burdigalinum*" [Pl. 13, fig. 10]). *Nassa veneris* Faujas de Saint-Fond, 1817 [Pl. 13, fig. 11] is the largest form in this heterogeneous group. It most closely resembles some species of the genus *Calophos* Woodring, 1964, except that it has a somewhat smaller and more multispiral protoconch (see p. 108).

While their actual species diversity and taxonomy remain obscure, it seems clear that these species do not comprise a single, closely related group. Most appear to be nassariid, and many resemble the species of the *Bullia* group more closely than species of Nassariinae. At least some should be seriously examined as possible close relatives of living *Dorsanum miran.* Many more are probably part of a radiation of European Tertiary Nassariinae and unrelated to the *Bullia* group. Others may belong in Buccinidae s. l., and still others to new or already recognized nassariid genera (*e.g.*, *Nassa veneris*). The phylogenetic discussion on pp. 100ff deals with only some of these taxa, and resolution of the status and taxonomic possibilities of most must await more detailed study.

Although the majority of these species have traditionally been placed in the genus *Dorsanum*, Baldi (1973) has referred the Oligocene species *Buccinum hungaricum* Gábor, 1936, to the genus *Bullia* (see Pl. 13, figs. 8, 9). Tables 12a and 12b list 53 trivial names assigned to *Dorsanum* by various authors and 12 assigned to the genus *Cyllenina* by Bellardi (1882). A large proportion of these designations will undoubtedly prove to be invalid upon revision. For the purposes of later diversity calculations, I have used what seems a conservative figure of 30 species for this group. In the remainder of this paper, I refer to all these species for convenience as "*Cyllenina*".

Genus **ANCILLOPSIS** Conrad, 1865a

Type species (by subsequent designation).—*Ancillopsis altilis* Conrad [Cossmann, 1899, p. 45].

"**Ancillopsis**" **patula** (Deshayes)
Plate 9, figure 12

Buccinum patulum Deshayes, 1835, p. 646, pl. 88, figs. 5, 6.
Buccinanops (*Brachysphingus*) *patulum* (Deshayes). Cossmann, 1901a, p. 48; Cossmann and Pissaro, 1904–1913, pl. 36, fig. 175-1.
Buccinanops patulum (Deshayes). Cossmann, 1901b, p. 222.
Ancillopsis patula (Deshayes). Gardner, 1945, p. 199.

Occurrence.—France, Paris Basin; U. K. [*fide* Cossmann, 1901b].

Range.—Upper Eocene (Auversian–Bartonian).

Material examined.—Specimen in collection of L. Dolin, St. Denis, France, from Ducy, near Montepilloy, France.

Remarks.—As noted by Palmer (1937, p. 289), this form bears remarkable resemblance to "*Bullia*" *altilis* and similar forms from the Eocene of the U. S. Gulf coastal plain. It is almost identical to some American individuals in its dorsoventrally flattened shape, minute spire, inflated, unsculptured body whorl, large aperture, expanded callus, and lack of terminal columellar fold. It is almost certainly related to the "*Bullia*" *altilis* complex, and points to a Lower Cenozoic geographic range for these forms that is as broad as for the *Bullia* group.

Neogene of Africa

Knowledge of Tertiary marine invertebrates from southern Africa is limited by the scarcity of Tertiary marine sediments in the region. One must, therefore, be especially cautious about conclusions drawn from the available sediments and fossils; patterns of diversity and distribution may not have been as they appear in the preserved record. Within this limited data base, the known fossil record of the *Bullia* group is itself limited. Table 13 summarizes all published occurrences of fossil and subfossil *Bullia* from southern Africa. The most important localities are indicated in Text-figure 20.

Newton (1913) described specimens from Redhouse, near Port Elizabeth, which he assigned to *Bullia annulata* (Lamarck, 1816a). On the basis of the molluscan fauna, he assigned a "Mio-Pliocene" age to the limestone from which they had been collected. Since Newton's time, the dating of these and other "coastal limestones" outcropping intermittently along the south and southwest coasts of the Cape Province has been controversial. From a review of all previous work, Dingle, Siesser, and Newton (1983, p. 268) conclude that these deposits "span a considerable part of the Cenozoic, generally progressing from older to younger beds in a seaward direction;" the marine facies of the sequence is probably late Miocene or early Pliocene in age.

Kensley (1972, 1977) has described invertebrate fossil assemblages from the Varswater Formation, exposed in quarries at Langebaanweg. The formation is divided into three members (Hendey, 1981a; Dingle, Siesser, and Newton, 1983). The basal Gravel Member

contains a diverse molluscan fauna interpreted by Kensley (1972; see also Dingle, Siesser, and Newton, 1983, p. 272) as indicative of intertidal marine environments with higher water temperatures than those prevailing off the southwest Cape at present. Kensley (1972) listed "*Bullia* sp." from the Gravel Member, later (Kensley, 1977) referring the material to *B. digitalis* (Dillwyn, 1817).

The Gravel Member is overlain by the Quartzose Sand Member, which contains abundant freshwater, terrestrial, and marine vertebrate and invertebrate fossils. Kensley (1977) lists three species of *Bullia* from this succession: *B. digitalis* (Dillwyn, 1817), *B. laevissima* (Gmelin, 1791), and an undescribed species. This last form appears to be distinct from any species of *Bullia* now living on the West Coast of South Africa, and may be an extinct species (Nuttall, written commun., 1985; Kensley, written commun., 1987).

The age of the Varswater Formation and its subjacent units has been the subject of some disagreement (Dingle, Siesser, and Newton, 1983, p. 278). Hendey concludes that the Gravel Member represents a late stage of a transgression which reached its peak in the middle or early late Miocene. Similarly, comparison with fossil mammal assemblages from Kenya suggests an early Pliocene age for the Quartzose Sand Member (Hendey, 1981a; Dingle, Siesser, and Newton, 1983, pp. 278–279).

The raised beach terraces of the coasts of Namibia and Namaqualand have proved to be productive

Table 13.—Published occurrences of fossil *Bullia* in southern Africa.

species	*locality*	*reference*	*Barnard locality*[1]
annulata	Redhouse, near Port Elizabeth	Newton (1913), Barnard (1959)	13
	raised beach, Mnandi Beach, False Bay	Kensley (1985b)	
callosa	Cape Cross salt pan, Southwest Africa (Recent)	Barnard (1959)	
digitalis	Angra Junta, Southwest Africa	Barnard (1959)	
	Sedgefield, near Knysna	Barnard (1959)	
	Cape Cross salt pan, Southwest Africa	Barnard (1959)	
	Langebaanweg, Cape	Kensley (1972, 1977)	
	Luderitz	Kensley (1972, 1977)	
	Orange River	Kensley (1972, 1977)	
	Keurbooms River	Kensley (1972, 1977)	
	raised beach at Mnandi Beach, False Bay	Kensley (1985b)	
cf. *diluta*	Durban		14
laevissima	Bogenfels, Angra Junta	Barnard (1959)	1, 2, 10, 13
	Sedgefield, near Knysna (Quaternary)	Barnard (1959)	
	Cape Cross salt pan	Barnard (1959)	
	Saldanha	Barnard (1959)	
	Langebaanweg, Cape	Kensley (1977)	
	raised beach at Mnandi Beach, False Bay	Kensley (1985b)	
magna	trench UV22, Uub Vlei	Haughton (1932)	2, 3
	Graauweduinen south (highest terrace)	Haughton (1932)	
	Doorn Bay (upper terrace)	Haughton (1932)	
mozambicensis	Mozambique		15
natalensis	raised beach at Durban-Umgeni	Barnard (1959)	14, 15
pura	raised beaches at Keurbooms River estuary	Barnard (1959)	5?
rhodostoma			5?
similis	raised beach (375′) at Durban-Umgeni	Barnard (1959)	14
n. sp.	Langebaanweg, Cape	Kensley (1977); Nuttall (written commun.)	
tenuis[2]	trench XVIIb, Oranjemund (main terrace)	Haughton (1932)	12
	trench XVIII, Oranjemund (advanced terrace)	Haughton (1932)	
	Graauweduinen south	Haughton (1932)	

[1] Localities listed by Barnard (1962, pp. 188–189), with original reference(s) or source of material: 1. Kaokoveld coast, north of Ugab River, probably near Cape Frio, raised beach (S. African Museum). Cape Cross, SW Africa (Gevers, 1932); 2. Bogenfels, Angra Junta, Uub Vlei, Oranjemund, SW Africa (between Luderitz and Orange River) (Haughton, 1932); 3. Alexander Bay, Port Nolloth, Graauweduinen, Klip Vlei, The Point, Little Namaqualand (between Orange River and Olifants River) (Haughton, 1932); 4. Doorn Bay, south of Olifants River (Haughton, 1932); 5. Velddrift, Berg River (St. Helena Bay); 6. Saldanha Bay, Hoedjies Bay, Geelbek (Haughton, 1932; Wybergh, 1920); 7. Wortel Gat, south of Klein River estuary, Stanford (Wybergh, 1920; South African Museum); 8. DeHoop, Rietvlei (Windhoek), Port Beaufort, Bredasdorp Division Arniston (Wybergh, 1920; South African Museum); 9. Little Brak River, Mossel Bay (South African Museum); 10. Sedgefield, west of Knysna (Martin, 1956; Barnard, 1959); 11. Knysna, raised beach (South African Museum); 12. Knysna District, Keurbooms River estuary, Jeffrey's Bay (South African Museum); 13. Algoa Bay area, Shark River, the Creek (Ferreira's River, Zwartkops River, Redhouse, Coega River, Coerney, Bushman's River (Stow, 1871; Johnson, 1904; Newton, 1913). Needs Camp, Buffalo River, East London (Newton, 1913); 14. Durban (Krige, 1933); 15. Inhambane District, Mozambique.

[2] Barnard (1959, 1962) believed that this is misidentified and actually belongs to *Bullia digitalis*.

sources not only of diamonds, but also of Late Tertiary and Quaternary fossils (Carrington and Kensley, 1969; Kensley, 1985c; Kensley and Pether, 1986). The value of these fossils is limited, however, by the difficulty in dating and correlating the various terrace deposits. The terraces reflect changes in sea level in southern Africa throughout the Late Cenozoic. Variations in altitude along the coast appear to be due to differential crustal warping during the same period (Dingle, Siesser, and Newton, 1983, p. 282). Higher terraces are older than lower terraces, the oldest dating back not earlier than the early Pliocene or late Miocene (Hendey, 1981b). Barnard (1959, 1962; see also Haughton, 1932) listed several species of *Bullia* from these deposits at various localities along the coast. Kensley and Pether (1986) summarize recent work on the fauna and biostratigraphy of these raised beaches. They report the occurrence of specimens of *Bullia annulata* (Lamarck, 1816a) from the "50 meter complex" at Hondeklipbaai, to which they assign a late Pliocene age.

The only species of South African *Bullia* thus far described solely from fossil material is *B. magna* Haughton, 1932 (Pl. 2, fig. 4). The original description is as follows:

> The shell is characterized mainly by its large size and massive build, by the straightness of the outline of the whorls and by the shape of its mouth. The largest complete shell has a height of 54 mm . . . The whorls are almost straight, very slightly convex, sculptured with approximately 24 low spiral ribs, which are visible only as colour bands in the specimens examined. No axial sculpture is visible. Post nuclear whorls fewer than in most species from South African waters. Angle of [spire] more acute than that of *B. laevissima* but greater than that in [*digitalis*]; spire blunt. Aperture large, wider than in [*digitalis*], approximately of the same shape as in *B. Natalensis*. The inner lip of the aperture is smooth, but the [posterior] dorsal margin of the shell above the [posterior] canal is thickened with callus. There is also a definite ring of callous thickening behind the [posterior] margin of each whorl. (Haughton, 1932, p. 47)[33]

This form has been found primarily in prospect trenches cutting through raised beach terraces, and so may be as old as Mio-Pliocene, but is probably younger. Barnard (1959, pp. 129–130) accepted *B. magna* as a valid taxon, commenting that, "Except for the absence of shoulders the shells might be *annulata* . . . but the parietal callus forms a ring behind the posterior margin of each whorl which it does not in *annulata*." In 1962, however, on the basis of his examination of more specimens, including the type of *B. magna*, Barnard considered *magna* to be "only worn and fossilized *annulata*" (Barnard, 1962, p. 182). Kensley and Pether (1986, p. 188) have studied still further material that, they claim, "removes any doubt that *Bullia magna* is *Bullia annulata*."

As important as where *Bullia* fossils have been found in southern Africa is where they have not. Two of the subcontinent's richest Tertiary faunas, for example, appear to lack any representative of *Bullia* s. s. The most diverse Tertiary macroinvertebrate assemblage known in southern Africa is that of the "*Pecten* bed", a four-to-five-meter thick limestone unit best exposed at Uloa in Zululand. King (1953, 1970) reported over 100 species (mostly mollusks) from these sediments. Based on the overall fauna, King (1953) suggested an early Miocene date for the *Pecten* bed. Frankel (1968) suggested a middle or late Miocene to Pliocene age based on sharks' teeth and foraminifera. More detailed examination of calcareous nannofossils and foraminifera has led Stapleton (1977) and Siesser and Miles (1979) to favor a late Miocene or early Pliocene age (see Dingle, Siesser, and Newton, 1983, pp. 258–259). No shells resembling *Bullia* are known from this assemblage.

Paleogene rocks are especially poorly represented by continental exposures in southern Africa. No Paleocene is known at the surface at all. Two small outliers of Eocene strata occur southwest of East London at Birbury and in a quarry at Needs Camp (Lock, 1973; Dingle, Siesser, and Newton, 1983, pp. 247–249). The upper bed at Needs Camp has recently been dated by calcareous nannofossils as probable early Eocene (Siesser and Miles, 1979). The macrofauna here is one of the richest so far described from the South African Paleogene (Dingle, Siesser, and Newton, 1983), but no representatives of the *Bullia* group have been reported.

Böhm (1926) provided an account of the macrofossils found in Tertiary sediments north and northeast of Bogenfels, on the west coast of southern Africa. Siesser and Salmon (1979) have proposed a late Eocene age for these strata on the basis of calcareous nannofossils and foraminifera. Bivalves and gastropods comprise the most diverse and abundant components of the assemblages, but nothing resembling *Bullia* has been described.

Haughton (1969, p. 436) cited H. Merensky as having identified "[fossils] from Elizabeth Bay as belonging to the genera *Bullia* and *Thais*," and as having suggested that the deposits in which these specimens were found were of Cretaceous age. It is far more likely, as Haughton realized, that they came from one of the raised terraces and are no older than Mio-Pliocene.

The following seem to be reasonable conclusions about the fossil record of *Bullia* in southern Africa:

(1) A substantial number of living species are represented by fossils of at least Pleistocene, and probably Pliocene age.

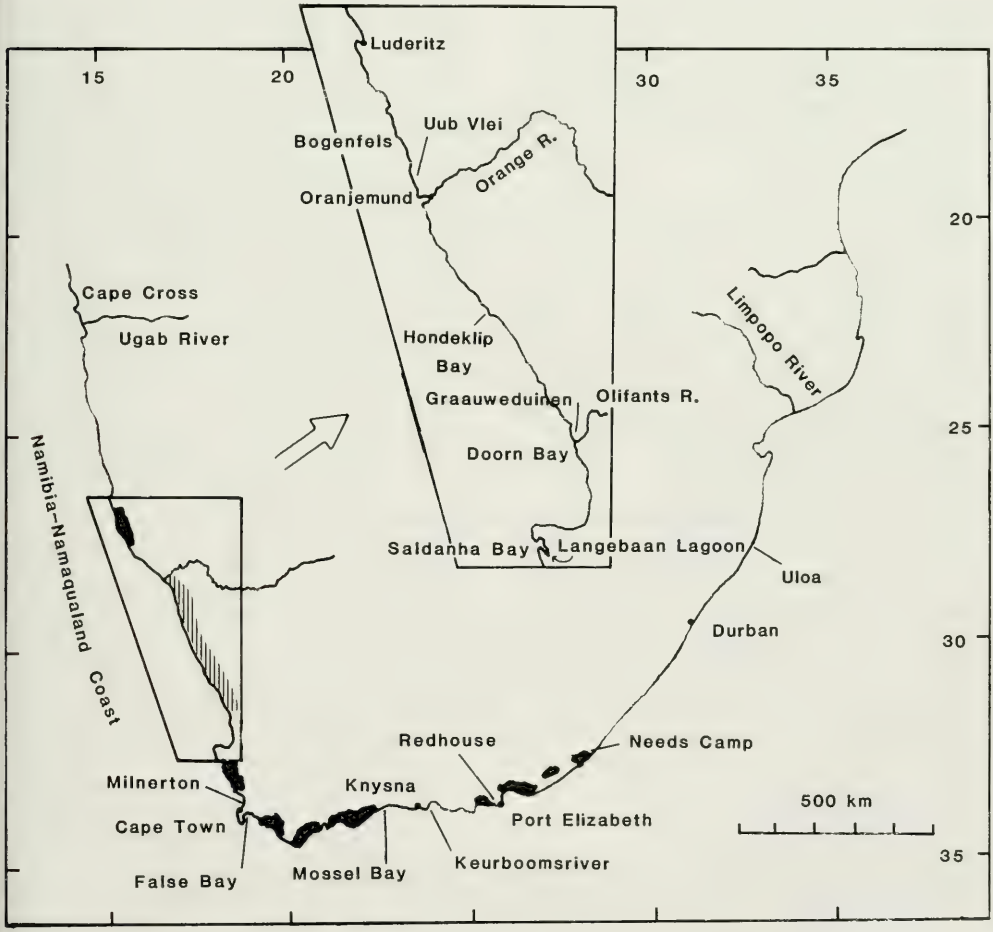
[33] Barnard (1962) proposed that Haughton's description be corrected by reading "*digitalis*" for "*tenuis*" because of Haughton's use of Tomlin's erroneous identification, and "posterior" for "anterior" to correct a simple terminological error.

(2) The oldest known representatives of the *Bullia* group in southern Africa are no older than late Miocene, and these are very similar or identical to living species; no members or obvious ancestors of the group have been found in pre-Mio-Pliocene rocks.

(3) There are very few or no known extinct species of *Bullia* from South Africa. The great majority, and perhaps all, of the specimens of fossil *Bullia* appear to belong to Recent species.

NEOGENE OF THE INDIAN SUBCONTINENT

Representatives of the *Bullia* group are known as fossils on the Indian subcontinent, but occurrences are rare. The only definite pre-Pliocene occurrence is that of "*Cominella annandalei*" Vredenburg, 1925, from the lower Oligocene of Pakistan. This species has been tentatively assigned to the genus *Keepingia* by Nuttall and Cooper (1973) (see p. 83). Apparently direct ancestors of the *Bullia* species inhabiting Recent Indian coasts are unknown until the Pliocene. Crame (1984) reports the following occurrences from the Mekran coast of Pakistan: lower? Pliocene (Talar Sandstone, Hingol Section), *Bullia* cf. *kurachensis* Angas, 1877, *B.* cf. *mauritiana* Gray, 1839, *B.* cf. *nitida* Sowerby, 1895,



Text-figure 20.—Map of southern Africa showing localities where fossil specimens of *Bullia* have been found.

B. cf. *tahitensis* (Gmelin, 1791)[34], *B.* sp. A, *B.* sp. B, *B.* sp. C, and *B.* sp.; Pleistocene (Jabal Haro sandstones, Hingol Section), at least three extinct *Bullia* species.

PHYLOGENY, BIOGEOGRAPHY, AND EVOLUTION

Phylogenetic Analysis and Paleontology

It has long been an assumption of most paleontologists, and many neontologists as well, that the phylogeny of a group of organisms can be more or less directly "read" from its fossil record. Defending this view, Simpson (1975, pp. 10–11) wrote that he considered it "self evident that when relevant fossils are available and are well interpreted, their characteristics and their succession provide both the most direct and the most important data bearing on phylogeny." This idea has, however, been challenged recently by workers on both sides of the fossil record on the grounds that fossils may not always be a sufficient or reliable source of phylogenetic information.

The problem of method in phylogenetic analysis is particularly acute in the case of fossil gastropods. Most systematic work on living prosobranchs depends on examination of soft anatomy, a complex of characters normally unavailable to the paleontologist. Gastropods are, however, among the most diverse and abundant groups of fossil organisms, and many basic aspects of their phylogeny are not yet understood. Most previous attempts at elucidating particular phylogenetic relationships and evolutionary pathways between living and fossil gastropod taxa have relied on little more than a seldom- or poorly-articulated combination of overall conchological resemblance and stratigraphic position. Little or no attention has been paid to issues of reliability, testability, or methodology, and most results have not been especially compelling. In light of this situation, it is appropriate to discuss methods of phylogenetic analysis in paleontology in some detail here, particularly as they pertain to the study of fossil gastropods.

Some of the strongest criticisms of traditional paleontological methods have come from practitioners of the "phylogenetic" or cladistic school of systematics. Under cladistic methods, fossils are no more important in analyzing evolutionary relationships of a group than are living forms. All taxa, living and extinct, are treated equally. Partly in response to criticisms of cladists, some paleontologists favor the "stratophenetic" approach. The term was coined, and the concept elaborated upon, by Gingerich (1976a, 1976b, 1979), and has also been discussed by Bretsky (1975, 1979), Prothero and Lazarus (1980) and Lazarus and Prothero (1984), among others. The basic thesis of this school is that fossils are of fundamental and unique importance in reconstructing phylogenetic relationships. The actual reliability and utility of the fossil record in any particular case, however, is dependent upon the completeness of that record; stratigraphic position is a reliable guide to phylogenetic position only when the record is "relatively dense and continuous" (Gingerich, 1979).

I approach phylogenetic analysis involving fossil taxa with the assumption that the fossil record can and does provide unique and important evidence useful in making phylogenetic inferences. I also believe, however, that previous workers subscribing to this view have not paid sufficient attention to the completeness of the available record, or to the effects of incompleteness on phylogenetic methods and assumptions. Phylogenetic inferences based solely or largely on the stratigraphic and geographic position of known fossils have a probability of being correct proportional to the quality of the record. When the record is poor, an atemporal, strictly morphological analysis has a higher probability of yielding correct results. The success of phylogenetic inference based only on a cladistic analysis of morphology, however, will also be limited if the organisms of interest lack abundant, discrete, hierarchically nested characters not prone to homoplasy. Here I suggest that the degree to which cladistic and stratophenetic methods are used should be dependent upon the nature of the stratigraphic and morphological evidence available in each case (Allmon, 1989).

Reconstructing phylogeny by this intermediate approach involves consideration of four questions: (1) how complete is the fossil record in the particular case?; (2) what types of morphological characters are actually available and should be used for phylogenetic analysis, and in what manner?; (3) how can direction of change (*i.e.*, polarity) in the characters considered be determined?; and (4) how can ancestor–descendant series be specified in phylogenetic trees? Each of these questions is dealt with separately below, in the context of a phylogenetic analysis of the fossil and living taxa of the *Bullia* group.

Completeness of the Fossil Record

Phylogenetic analysis based on a given fossil record can only be as good as that fossil record. A concept of

[34] Cernohorsky (1984, p. 29) discusses morphological features of this form that indicate it may not belong to *Bullia* s. s.:

> If really a true *Bullia*, then the type locality [Tahiti] is erroneous, since *Bullia* does not live in the Pacific Ocean . . . Recent authors have adopted the name *Bullia tahitensis* and credited the authorship to either Gmelin or Gray, but the taxon *B. othaeitensis* (Bruguière) is chronologically prior and should be used for a taxon which cannot be unequivocally identified and should be considered a *nomen dubium* or *nomen inquirendum*.

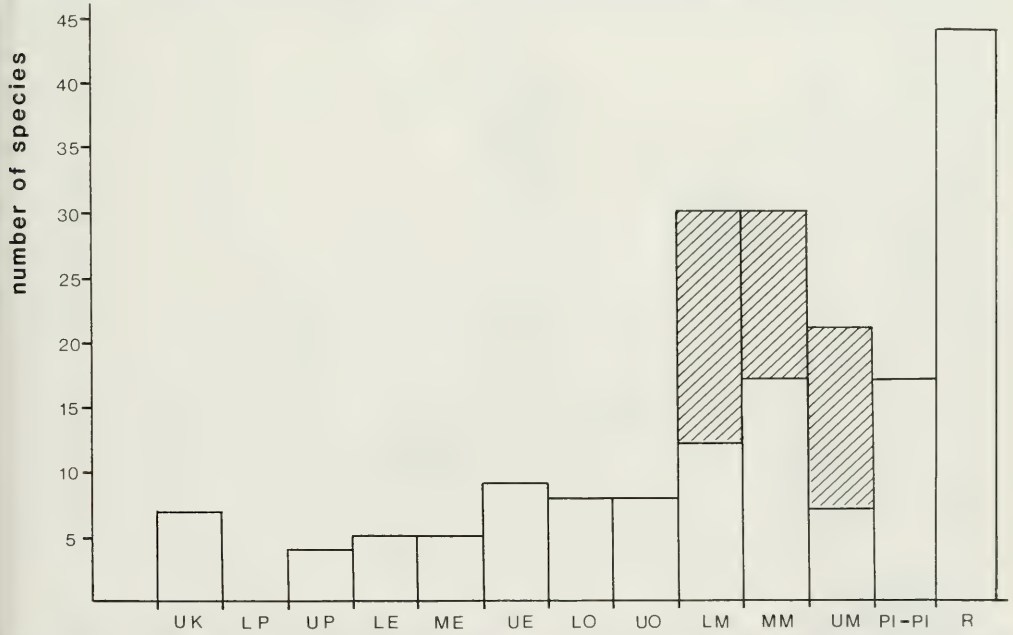
fossil record quality, or "paleontological completeness", is therefore required. For purposes of phylogenetic analysis, paleontological completeness can be defined as "the proportion of the total time and space inhabited by all the individuals of all the species of the group of interest that is preserved by fossils" (Allmon, 1989). This concept encompasses three phylogenetically important aspects of the completeness problem (Bretsky, 1979): (1) completeness of species diversity; (2) completeness of stratigraphic duration of known species; and (3) completeness of geographic range of both individual species and the entire group.

Each of these aspects should be considered at stratigraphic and geographic scales appropriate for the taxonomic level and phylogenetic question of interest. For lower taxonomic levels within single basins or provinces, techniques of stratigraphic completeness measurement can be adopted to estimate paleontological completeness. In cases of higher taxa over larger stratigraphic and geographic intervals, such methods are impractical and others are required.

Bretsky (1979) proposed a method for estimating completeness of species diversity for West Atlantic Tertiary lucinid bivalves. She compared the observed diversity of fossil species throughout the Tertiary to known Recent species diversity, found approximate correspondence, and concluded that this record is "dense and continuous" enough to employ the stratophenetic method in a phylogenetic reconstruction (Bretsky, 1979, pp. 126–127).

The pattern of diversity in the fossil record of the *Bullia* group differs in several respects from that of the Recent species. Text-figure 21 shows the stratigraphic distribution of all species considered here to be probable members of the *Bullia* group. The number of known species existing throughout the Cenozoic is represented in Text-figure 22. Species of the group occur today in two areas (western and southern Africa east to India, and southernmost South America). Forty-four living species are recognized as belonging to the group, approximately 75% of which belong to a single subgenus (see Table 3a). While there are certainly some divergent taxa (*e. g.*, several Indian Ocean species of *Bullia* s. s.), the range of basic morphological diversity is not large.

The fossil forms suggested here to belong to the *Bul-*



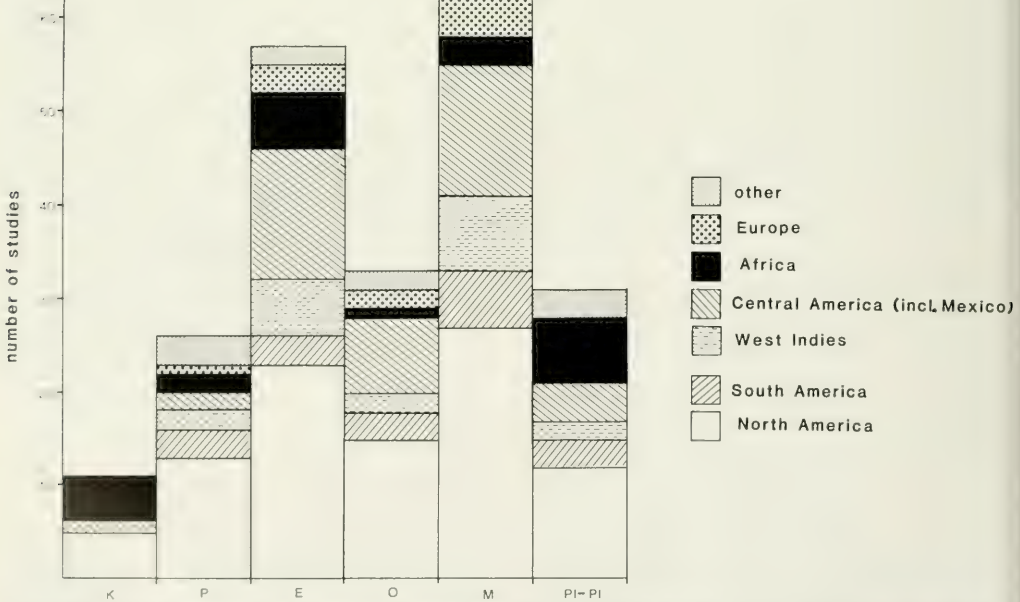
Text-figure 22.—Histogram showing the number of species of the *Bullia* group from the Upper Cretaceous through the Recent. The shaded area represents one-half of the total number of described species from the European Tertiary here informally referred to as *Cyllenina* (data from Table 3a). UK = Upper Cretaceous; LP = lower Paleocene; UP = upper Paleocene; LE = lower Eocene; ME = middle Eocene; UE = upper Eocene; LO = lower Oligocene; UO = upper Oligocene; LM = lower Miocene; MM = middle Miocene; UM = upper Miocene; Pl–Pl = Plio-Pleistocene; R = Recent.

lia group, in contrast, show a much broader total geographic distribution, ranging across the North and South Atlantic, into the Caribbean and eastern Pacific, and occurring on at least four continents. Between 60 and 80 fossil species are suggested as belonging to the group. Although this is higher than the total number of Recent species, Text-figure 22 shows that total species diversity is probably higher today than at any other single time in the history of the group. The majority of Recent species, however, belong to *Bullia* (*Bullia*), while in the Eocene and lower Miocene as many as four or five genus-level taxa, each with relatively few species, may have existed simultaneously.

The structure and levels of diversity within the group thus seem to have changed significantly during its history. Bretsky's (1979) method for estimating the completeness of species diversity is therefore inappropriate for these gastropods; diversity in the present appears to be an insufficient guide to diversity in the past.

I propose here an alternative method, which may be referred to informally as the "faunal survey" method, for estimating paleontological completeness for relatively long-lived and widespread higher taxa. This approach is similar to that discussed briefly by Simpson (1940) in his summary of the evolution and biogeography of mastodonts. Simpson suggested that mastodonts evolved in Africa during the Oligocene and spread to Europe in the early Miocene and North America in the late Miocene. He supported this claim by pointing out that there were many Oligocene vertebrate faunas known from outside Africa, "and it is inconceivable that mastodonts or any possible ancestors of mastodonts would be (as they are) entirely unknown in [these faunas] if they already had anything comparable to the maximum distribution" (Simpson, 1940, p. 142).

A crude estimate of what proportion of all species from throughout the geological history and geographical range of a group has been preserved in the fossil record can be made by examination of the monographic literature. I have examined as many published molluscan faunas from the circum-Atlantic region as possible, spanning as much of the Cenozoic as possible, and searched for taxa that might belong to the *Bullia* group. I looked in taxonomic indices for the following names: *Ancillopsis*, *Ancilla*, *Brachysphingus*, *Buccinanops*, *Buccinopsis*, *Bullia*, *Bulliopsis*, *Calophos*, *Dorsanum*, *Molopophorus*, *Nassa*, and *Perunassa*. Most of the taxa were located in this way or through cross-



Text-figure 23.—Histogram showing the stratigraphic and geographic distribution of published fossil faunas examined in this study (data from Table 14). UK = Cretaceous; P = Paleocene; E = Eocene; O = Oligocene; M = Miocene; Pl–Pl = Plio-Pleistocene.

Table 14.—Published taxonomic works consulted in the "faunal survey" method of estimating completeness of the fossil record of the *Bullia* group. This list includes only the most recent faunal revisions of each area available, and so in most cases does not include superceded older works.

reference	*locality*	*age*
Abbass (1967)	Egypt	Paleocene–Eocene
Addicott (1970)	California	Miocene
*Addicott (1976)	Oregon, Washington	Miocene
*Addicott (1978)	British Columbia	Miocene
Adegoke (1969)	California	Neogene
Adegoke (1977)	Nigeria	Tertiary
*Anderson (1929)	Colombia	Miocene
*Anderson and Martin (1914)	California	Neogene
*Arnold (1907)	California	Tertiary
*Arnold (1908)	California	Cretaceous–Tertiary
*Arnold and Hannibal (1913)	northwestern North America	Tertiary
*Baldi (1973)	central Europe	Oligocene
Barber (1958)	Nigeria	Cretaceous
*Barnard (1959)	South Africa	Plio-Pleistocene
*Barnard (1962)	South Africa	Plio-Pleistocene
Böhm (1926)	South Africa	Tertiary
*Böse (1906)	Mexico	Tertiary
*Carrington and Kensley (1969)	South Africa	Pleistocene
*Clark (1915)	California	Miocene
*Clark (1918)	California	Miocene
*Clark (1938)	California	Eocene
Clark (1946)	Colombia	Eocene
*Clark and Arnold (1923)	British Columbia	Oligocene
Clark and Durham (1946)	Colombia	Eocene
Clark and Woodford (1927)	Colombia	Eocene
Clark (1906)	Maryland	Plio-Pleistocene
Clark and Martin (1901)	Maryland	Eocene
Cooke (1919)	West Indies	Tertiary
Cossmann and Pissaro (1904–1913)	France	Eocene
Cox (1952)	Gold Coast	Cretaceous–Tertiary
*Dall and Ochsner (1928)	Galapagos	Pliocene
*Dickerson (1915)	California	Eocene
*Dickerson (1916)	California	Eocene
Dockery (1977)	Mississippi	Eocene
Dockery (1980)	Mississippi	Eocene
*Durham (1944)	Washington	Oligocene
Eames (1957)	Nigeria	Eocene
*Effinger (1938)	Washington	Oligocene
*Etherington (1931)	Washington	Miocene
Feruglio (1936)	Patagonia	Tertiary
Fleming (1972)	Chile	Plio-Pleistocene
Gardner (1926–1947)	Florida	Pliocene
Gardner (1935)	Texas	Paleocene
Gardner (1945)	Mexico	Tertiary
Gardner (1948a)	Maryland	Miocene
*Gardner (1948b)	Virginia, North Carolina	Mio-Pliocene
*Givens (1974)	California	Eocene
Harris (1895a)	Texas	Paleogene
Harris (1895b)	Alabama	Eocene
Harris and Palmer (1946–1947)	southeastern United States	Eocene
*Haughton (1932)	South Africa	Plio-Pleistocene
Herm (1969)	Chile	Neogene
Hertlein (1972)	Galapagos	Pliocene
Hertlein and Strong (1939)	Galapagos	Pleistocene
*Hickman (1969)	Oregon	Oligocene
*Hickman (1980)	Oregon	Paleocene
*Hilber (1879)	central Europe	Miocene
*Hoernes and Auinger (1882)	central Europe	Miocene
*Hölzl (1958)	central Europe	Miocene
Howe (1922)	Oregon	Pliocene

Table 14.—Continued.

reference	*locality*	*age*
*Ihering (1907)	Patagonia	Tertiary
*Jekelius (1944)	Romania	Miocene
Jung (1965)	Venezuela	Miocene
*Jung (1969)	Trinidad	Mio-Pliocene
Jung (1971)	West Indies	Eocene
Jung (1974)	West Indies	Eocene
Kensley (1972)	South Africa	Pliocene
*Kensley (1977)	South Africa	Pliocene
*Kensley (1985a)	South Africa	Pliocene
*Kensley (1985b)	South Africa	Pliocene
*Kensley and Pether (1986)	South Africa	Plio-Pleistocene
King (1953)	South Africa	Mio-Pliocene
King (1970)	South Africa	Mio-Pliocene
King (1972)	South Africa	Pliocene
Kollmann and Peel (1983)	Greenland	Paleocene
Kugler and Caudri (1975)	Trinidad	Eocene
LeBlanc (1942)	Louisiana	Eocene
Lock (1973)	South Africa	Eocene
Loel and Corey (1932)	California	Miocene
MacNeil and Dockery (1984)	Mississippi	Oligocene
*Malumian, Camacho, and Gorroño (1978)	Patagonia	Tertiary
Mansfield (1925)	Trinidad	Miocene
*Mansfield (1930)	Florida	Miocene
Mansfield (1937)	Florida	Miocene
Mansfield (1940)	Alabama, Mississippi	Oligocene
*Marincovich (1983)	Alaska	Miocene
Marks (1951)	Ecuador	Miocene
*Martin (1904)	Maryland	Miocene
Maury (1912)	Trinidad	Miocene
*Maury (1917)	Dominican Republic	Miocene
Maury (1924–1927)	Brazil	Tertiary
Merriam and Turner (1937)	California	Eocene
*Moore (1963)	Oregon	Miocene
*Moore (1976)	Oregon	Oligocene
*Nelson (1925)	California	Eocene
*Newton (1913)	South Africa	Tertiary
Newton (1922)	Nigeria	Eocene
*Nuttall and Cooper (1973)	western Europe	Paleogene
Olsson (1922)	Costa Rica	Miocene
*Olsson (1928)	Peru	Tertiary
Olsson (1929)	Peru	Eocene
Olsson (1930)	Peru	Oligocene
*Olsson (1932)	Peru	Miocene
Olsson (1942)	Panama, Costa Rica	Tertiary
*Olsson (1964)	Ecuador	Neogene
Olsson (1967)	Florida, Caribbean	Tertiary
Olsson and Harbison (1953)	Florida	Pliocene
*Olsson and Petit (1964)	southeastern United States	Neogene
Ortmann (1900)	Patagonia	Tertiary
Ortmann (1902)	Patagonia	Tertiary
*Palmer (1937)	southeastern United States	Eocene
*Perrilliat Montoya (1963)	Mexico	Miocene
*Peyrot (1925–1926)	France	Miocene
Philippi (1887)	Chile	Tertiary
Pilsbry (1922)	Dominican Republic	Tertiary
*Pilsbry and Olsson (1941)	Eucador	Miocene
Plummer (1932)	Texas	Tertiary
Price and Palmer (1928)	Texas	Eocene
Ravn (1904)	Greenland	Tertiary
Ravn (1939)	Denmark	Paleocene
Rennie (1929)	Angola	Cretaceous

Table 14.—Continued.

reference	*locality*	*age*
Rennie (1945)	Angola	Cretaceous
*Richards (1947)	eastern United States	Miocene
*Richards and Harbison (1942)	New Jersey	Miocene
Richards and Palmer (1953)	Florida	Eocene
Rosenkrantz (1970)	Greenland	Tertiary
Rossi and Levy (1977)	Argentina	Eocene
Rutsch (1929)	Switzerland	Miocene
*Rutsch (1942)	Trinidad	Miocene
Sheppard (1937)	Ecuador	Eocene
*Sohl (1964)	southeastern United States	Cretaceous
*Squires (1984)	California	Eocene
*Steinmann and Wilckens (1908)	Tierra del Fuego	Tertiary
*Strausz (1966)	central Europe	Miocene
Tegland (1933)	Washington	Oligocene
*Toulmin (1977)	Alabama	Paleogene
Trechmann (1923)	Jamaica	Tertiary
*Tucker and Wilson (1932a, 1932b)	Florida	Tertiary
Tucker and Wilson (1933)	Florida	Neogene
*Turner (1938)	Oregon	Eocene
*Vokes (1939)	California	Eocene
*Wagner and Schilling (1923)	California	Miocene
Weaver (1912)	Washington	Tertiary
Weaver (1931)	Argentina	Jurassic–Cretaceous
*Weaver (1942)	Washington	Tertiary
Weisbord (1929)	Colombia	Miocene
Weisbord (1962)	Venezuela	Neogene
Wilbert (1953)	Arkansas	Eocene
*Wilckens (1911)	Antarctica	Tertiary
Woodring (1928)	Jamaica	Miocene
*Woodring (1964)	Panama	Miocene
Woods (1906)	South Africa	Cretaceous
*Woods (1922)	Peru	Tertiary
*Zelinskaya *et al.* (1968)	eastern Europe	Paleogene

* Faunas containing representatives of the *Bullia* group.

citation from other works. A certain number were also found by examining plates for familiar-looking morphologies. Table 14 lists the published taxonomic works consulted (151 in all). Their stratigraphic and geographic coverage are represented in Text-figure 23. This paper represents a compilation and preliminary analysis of the affinities of these potential members.

The largest gap in the fossil record of the group occurs between the end of the Cretaceous and the beginning of the upper Paleocene, a period of approximately nine million years (approximately 10% of the group's total history). Sediments of the Midway Group of the Gulf coastal plain of the U. S. were deposited during this time, but their faunas do not appear to include representatives of the *Bullia* group (Harris, 1896; Plummer, 1932; Gardner, 1935). Further work will undoubtedly show these older faunal lists to be incomplete, but they are all that is available at present. Lower Paleocene faunas from elsewhere in the circum-Atlantic are even more poorly known and no other major sources of taxonomic information from this period of time are available.

The fossil molluscan faunas of the Eocene of the Gulf Coast of the U. S. were considered in some detail beginning on p. 53, and only a single species from these faunas [*Bulliopsis choctavensis* (Aldrich, 1886)] is believed to be assignable to the group. Similarly, the well-known faunas of the Eocene of the Paris Basin (Cossmann and Pissaro, 1904–1913) appear to contain no representatives of the *Bullia* group.

In North America, a major gap in the record of the group occurs between the middle Eocene and middle Miocene. Much of this gap may be due to a paucity of Oligocene and lower Miocene sediments. This period is in general a time of low sea-level stand and abundant well-preserved mollusk faunas are rare worldwide. It may be noted, however, that a major recent monograph on the gastropods of the lower Oligocene Vicksburg Group of the Gulf coastal plain (MacNeil and Dockery, 1984) contains no taxa referable to the *Bullia* group. This is then a period of as much as 15 million years for which there is no record of the group in North America, although a number of species are known from elsewhere. Whether this gap is real, or an artifact of

preservation, is presently unknown.

Of particular interest is the Cenozoic record in Africa. With the possible exception of a single problematic form from West Africa [*Desorinassa? bonnecarrei* (Furon *in* Furon and Kouriatchy, 1948); see Table 3a], there are no known fossils of any member of the *Bullia* group dating from earlier than Pliocene. As discussed above, this may be due in large part to a lack of pre-Neogene sediment over much of the African continent. It was also pointed out, however, that several diverse Eocene molluscan faunas are known from southern Africa, but that they appear to lack representatives of the group. A similar pattern seems to hold for southern South America.

Lack of known fossil representatives in a certain region at a certain time, therefore, could be due to: (1) true absence of the group; (2) lack of sedimentary record; (3) lack of fossils in sediment; (4) lack of knowledge of fossils present; or (5) extreme rarity. To decide whether the first of these was in fact the case, the contributory effects of the other four must be estimated, considering them as relative factors rather than as absolute conditions.

Lack of sediment of appropriate age may contribute to paucity of pre-Plio-Pleistocene record of the group in southern Africa, and to the low number of Oligocene taxa in the Americas. These regional hiatuses may comprise as much as 30% of the total potential record of the group. Although it is possible for gastropods to be leached away when other fossils (*e.g.*, calcitic bivalves) remain, and the effects of these processes on the resulting available record are distressingly difficult to quantify, *Bullia* group shells are about as sturdy as those of any gastropod, and it is reasonable to assume that they would usually be preserved if present. Lack of monographic knowledge of certain times and regions is always a problem, but is relatively less so for Tertiary gastropods of the circum-Atlantic than for many other fossil groups. There are few major intervals of time since the Late Cretaceous unrepresented in Table 14 by a major study of marine mollusk faunas. The effects of actual rarity are more difficult to estimate. Perhaps all that can be said is that for a group such as *Bullia* and kin, which has apparently never been abundant in any fauna, more caution should be used in concluding that it is absent from a fauna than for a group that is more often locally abundant.

Although it is no more than a rough estimate, from the foregoing analysis I suggest that between 60 and 90% of the species of the *Bullia* group are represented in the known fossil record as presented in Text-figure 21.

How inaccurate are the observed species ranges? By its use of literature rather than occurrence information gathered firsthand, the approach used here has a built-in source of potential imprecision and inaccuracy concerning actual stratigraphic ranges. Published species ranges are seldom more precise than to stage level, particularly in older literature, and often are much coarser in their resolution. The length of some stratigraphic ranges plotted in Text-figure 21 reflects little more than the error bar for the dating of the formation in which the species occurs.

The stratigraphic "range" of any fossil species is made up of a number of discrete occurrences, usually in separate localities and in strata whose exact correlation may be problematic. In Text-figure 21, plotted ranges may be derived from single occurrences, or even single specimens [*e.g.*, "*Dorsanum*" *lagunitense* (Woods, 1922)], multiple, widely spaced occurrences of abundant specimens ("*Molopophorus*" spp.), or simply published ranges (most European species), that vary in precision from partial stage to epoch.

How much does this varying precision affect our confidence in Text-figure 21 as a reliable guide to stratigraphic ranges of the fossil species in the group? This is dependent upon the scale of the questions being asked. At a very low taxonomic level (such as discussed on p. 30), the details of occurrence within total stratigraphic ranges, and the accuracy and precision of determining those ranges, are critical. At higher taxonomic and temporal scales, however, increasingly coarse information becomes useful. In this paper I ask what the chances are that the observed stratigraphic ranges of supraspecific groups are reliable indicators of actual stratigraphic ranges of these taxa. This is similar to the "probabilistic" approach to phylogenetic data favored by Lazarus and Prothero (1984). The method used here suggests that, at approximately the level of the stage (*e.g.*, upper Miocene, lower Oligocene) these ranges seem unlikely to change very much. Future work will, of course, contribute to increased precision below this level, but it seems that, with some exceptions (*e.g.*, the lower Paleocene, much of the Oligocene, the lower Miocene in North America), our knowledge of Cenozoic molluscan faunas is complete enough to allow us to make some large-scale statements about the history of this group.

In summary, paleontological completeness estimates that the fossil record of the *Bullia* group falls into the "middle ground" of Fortey and Jefferies (1982, p. 209), in which the stratigraphic record is neither complete enough to serve alone as a sufficient and consistently reliable guide to phylogeny reconstruction, nor incomplete enough to be safely ignored without significant loss of valuable phylogenetic information.

CHARACTERS AND CHARACTER ANALYSIS

Character analysis in fossil gastropods must deal with at least four questions: (1) can phylogeny be reconstructed using only conchological characters?; (2) what individual shell characters can and should be used in a phylogenetic analysis?; (3) should different characters be given different weights?; and (4) what has been the frequency of homoplasy in these characters?

Ideally, estimates of the confidence with which shell characters can be used for gastropod systematics could be obtained from studies of Recent taxa in which hard and soft part character distributions have been compared. Such studies, however, are rare. As noted above on p. 8, although other data are potentially available, new species of *Bullia* s. s. continue to be described almost solely from shell characters, thereby making many Recent "species" no more or less reliable than fossil "species".

Ponder (1973) discussed both soft parts and shell morphology in his summary of neogastropod classification at and above the family level. Most general treatments of gastropod systematics at the species level, however, consider only conchological characters. In his monograph on Indo-Pacific species of Nassariinae, for example, Cernohorsky (1984) discusses only shell, opercular, and radular characters. Radwin and d'Attilio (1971) proposed a supraspecific taxonomy of Muricacea based on the shell and radula, and found a reasonable degree of concordance between these two character systems. Some degree of concordance between radular, shell, and soft-part characters is evident in the classification of living *Bullia* group species introduced on p. 19 herein. Schilder (1936) discussed anatomical characters in species of Cypraeacea that agreed with conchological characters. In a detailed study of the morphologically variable species *Rissoa auriscalpium* (Linnaeus, 1767), Colognola *et al.* (1986) found that subtle but consistent shell and radular differences were not reflected by electrophoretic analysis. These authors conclude that the nominal species in fact consists of two very similar but morphologically distinct species. Considering the classification of several subfamilies in the Volutidae, Clench and Turner (1964) stated that reliable taxonomic decisions could not have been made on the basis of shell characters alone. Similarly Hughes and Emerson (1987) summarize anatomical studies placing the genus *Morum* Röding, 1798 in the family Harpaidae, in contrast to shell characters conventionally used to assign it to Cassidae. Verduin (1984) states that in most members of Rissoidae, shell form alone is an adequate guide to species-level differences, but that lack of soft part and radular information presents serious problems for establishing generic and subgeneric divisions.

It may be that shell and radular characters are in fact the characters in which most prosobranch genera and species differ, while suprageneric taxa can be more easily distinguished on the basis of soft anatomy or genetic differences. This is implied by Ponder (1973, p. 302) when he states that features such as the shell, which deal with the external environment, "are often the first structures to be modified by it."

Shell characters may, therefore, be misleading in attempting higher-level classification of some gastropod groups, an unfortunate situation for paleontologists. A reasonable course of action is to use all available shell characters for classification and phylogenetic analysis of fossil gastropods, but to accept the results cautiously. Stratigraphic ordering of fossil taxa, their geographic and environmental distribution, as well as the nonshell characters of living relatives must also be taken into account where this information is available. The resolution of the relationship of species of the *Bullia* group to the family Melanopsidae, discussed briefly on p. 12, is an example of the use of such multiple criteria in classification of fossil taxa.

Another problem, common to all morphological analyses, is the definition of individual characters. This is particularly difficult in the case of gastropod shells where most characters are highly intercorrelated. Without detailed ontogenetic and developmental information, it is very difficult to say how many discrete characters are actually involved in a given phenotypic pattern. Homologies are difficult to define for the same reason. This situation exerts an effect of unknown magnitude on the phylogenetic analysis described below, and is another reason for approaching it with caution.

Homoplasy is a major obstacle to any attempt to reconstruct phylogeny (see, *e.g.*, Simpson, 1961; Mayr, 1981), but it is a particular problem for atemporal, strictly morphological (*i.e.*, cladistic) analyses (Felsenstein, 1978; Bretsky, 1979; Mayr, 1981; Panchen, 1982; Gosliner and Ghiselin, 1984). In cladistic methods, the preferred hypothesis of relationship is (by the principle of parsimony) the one exhibiting the greatest congruence of synapomorphies and the smallest amount of homoplasy or character reversal (Eldredge and Cracraft, 1980, pp. 67, 70), *i.e.*, the "shortest tree". This procedure will only work, however, if homology outnumbers analogy. If true synapomorphies cannot be distinguished from shared characters resulting from homoplasy, or if the number of homoplastic characters greatly outnumbers the truly derived characters, then cladistic methods will break down (or at least become much more difficult), and other criteria must be employed (Eldredge, 1979, pp. 185–186; Lazarus and Prothero, 1984).

The use of parsimony in phylogenetic analysis may be useful as a heuristic device, as long as it is realized that nature itself is not necessarily parsimonious (see, *e.g.*, Hecht, 1976; Wiley, 1981; Johnson, 1982; Marshall, 1986). In practice, however, choosing the hypothesis that minimizes homoplasy often involves the assumption that it is indeed minimal (Felsenstein, 1978; Gosliner and Ghiselin, 1984).

In an apparent defense of this reasoning, Farris (1983, pp. 12–14; see also Sober, 1983, and Schoch, 1986, p. 145) has claimed that, although the parsimony criterion requires that the phylogenetic hypothesis with the least amount of homoplasy be accepted, the use of parsimony in phylogenetic inference does not in fact depend on the supposition that homoplasy is truly rare in evolution. Farris' argument seems to be approximately as follows: all putative synapomorphies do not necessarily represent homologous characters; some may be the result of homoplasy. Only a single "true" (*i.e.*, homologous) synapomorphy is required to demonstrate the phylogenetic relationship of two taxa; all other characters uniting the two can be homoplastic without affecting this conclusion. Even in the extreme case, Farris concludes, if all characters considered are homoplastic, this would not falsify a particular phylogenetic relationship. "Under those circumstances the data would simply leave the question of the truth of that (or any other) grouping entirely open." (Farris, 1983, p. 13)

There are at least two problems with this argument. First, while it is indeed the case that a single "true" shared derived character could validate a phylogenetic hypothesis uniting two taxa, it cannot ever be known which synapomorphies are "true" and which are not. Given imperfect knowledge, phylogenetic inference by comparative morphology requires that putative homologous features uniting closest relatives outnumber analogous (*i.e.*, homoplastic) features. Although various methods allow us to put more confidence in some morphological features than in others as homologous, if homoplasy really does "swamp" shared derived characters in a group, then unweighted, atemporal morphology alone cannot be an accurate guide to phylogenetic relationships. Secondly, in concluding that in the extreme case of total homoplasy, no phylogenetic inferrence is possible at all, Farris neglects the potential of stratigraphic evidence to contribute to a resolution. A fossil record of sufficient quality can reveal homoplastic lineages, often allowing them to be linked stratigraphically and/or geographically to related lineages, and can fill a gap left when homoplasy overpowers conclusions based solely on morphology (see, *e.g.*, Simpson, 1961).

Homoplasy may in fact be widespread, and might even be described as a major evolutionary theme, in many groups of organisms. Newell and Boyd (1975, p. 61; cited in Lazarus and Prothero, 1984; see also Gould, 1970; Eldredge, 1979, p. 170n; Butler, 1982) conclude that "parallel trends constitute the general, not unusual phenomena inherent in the evolutionary process." It is significant that, as noted by several authors (*e.g.*, Bretsky, 1979, p. 117; Gosliner and Ghiselin, 1984), traditionally inclined morphologists and stratigraphical paleontologists tend to believe that homoplasy is common, while cladists have tended to de-emphasize its importance.

While the occurrence of homoplasy has been reported in a wide variety of groups, it seems to be of more importance in some groups than in others. The organisms that seem most prone to homoplasy are those of relatively simple structure; foraminifera, for example, appear to show more homoplasy than echinoderms. Campbell (1975, p. 89) suggests that cladistic methods are more useful in dealing with vertebrates than with invertebrates because vertebrates "have more complex skeletons with more intricate structures exhibiting more easily recognized shared-derived (specialized) characters." Lazarus and Prothero (1984) similarly consider foraminifera and other deep-sea microfossils to "lack a sufficient number of hierarchically nested sets of characters for cladistic analysis," and to show convergence and iterative evolution to such an extent that some characters may have arisen independently many times. Like foraminiferal tests, gastropod shells are geometrically very simple, and display fewer discrete and hierarchically arranged characters than do some other shelly macroinvertebrates (such as trilobites, ostracodes, or echinoderms, on which cladistic methods have been employed with some success (see, *e.g.*, Eldredge, 1973; Abdul-Razzaq, 1973; Smith, 1984; but see Erwin, 1988; Michaux, 1989). There are thus reasons for expecting, *a priori*, that homoplasy may be important in gastropods. There are furthermore many individual studies that suggest that homoplasy may be significant in gastropod evolution (*e.g.*, Yonge, 1938; Hubendick, 1952; Eldredge, 1968; Gould, 1969; Davis, 1979; Chambers, 1982; Gosliner and Ghiselin, 1984; Harasewych, 1984; Allmon and Geary, 1986).

The foregoing argument is not meant to imply that all aspects of gastropod shell form are equally prone to homoplasy. Based on knowledge of other groups, this seems unlikely; it is widely acknowledged that some morphological characters show less homoplasy than others, and this usually forms the basis for their being relied upon in classifications (*e.g.*, ammonoid sutures, mammal teeth). Hecht (1976) has ranked types of morphological features, according to his assessment of the relative likelihood of each of these types exhibiting

homoplasy. "Loss characters", particularly those which give little or no information to indicate the pathway by which the loss occurred (*e.g.*, blindness), he suggests, are especially likely to be homoplastic, and so of little or no use in phylogenetic inference (Eldredge, 1979, p. 173, states, however, that blindness is an "excellent synapomorphy" for the Cambrian trilobite family Conocoryphidae).

Certain features of gastropod shells will, therefore, probably be less prone to homoplasy than others. These patterns of character variation will vary in detail from group to group. It seems reasonable, however, to establish some guidelines at the outset. Based on their overall (and admittedly subjectively determined) "level of complexity", and within certain limits, specific to each group, overall geometry (see, *e.g.*, Raup, 1966) and external sculpture are probably more plastic than more discrete morphological features such as canals, channels, and folds. Individual decisions about such characters depend on determination of homology, which may be problematic without abundant developmental information. Homology would, however, seem to be easier to support for these more distinct characters than for the more general features of shape or sculpture. Wiley (1981, p. 141; see also Mayr, 1969, p. 220) has advocated such consideration of the "quality" of individual characters in phylogenetic analyses. As he also emphasizes, proposition of homology represents only the proposition of a hypothesis that should be subject to further testing.

POLARITY

Tradition holds that paleontology offers the best direct evidence of polarity in morphological sequences. Fossils found stratigraphically below others are usually presumed to show more primitive morphologies, younger forms to show more derived morphologies (see, *e.g.*, Simpson, 1961, 1975; Gingerich, 1979). Critics of this view maintain that, for most groups and most times, the fossil record is too incomplete to assure that what we see is an accurate representation of what really existed. If, for example, more advanced members (*i.e.*, those with more derived morphologies) of a clade become extinct before their more primitive cousins, then literal reading of an imperfect record could lead to a misleading representation of the polarity of the characters involved (Schaeffer, Hecht, and Eldredge, 1972; Eldredge, 1979; Eldredge and Cracraft, 1980).

Referring to Schaeffer, Hecht, and Eldredge (1972), Simpson (1975, p. 14) wrote, "The most important point of their argument is that primitiveness and ancientness are not necessarily correlated. This is true, but they *usually* are correlated, and for any group with even a fair fossil record there is seldom any doubt that characters usual or shared by older members are almost always more primitive than those of later members." [emphasis in original] A similar view has been expressed by Mayr (1981, p. 512), and also by Wiley (1981, p. 149), who states that "It cannot be denied that geologic age and plesiomorphy (*i.e.*, primitiveness) are highly correlated."

The effects of noncorrelation between primitiveness and antiquity on determination of polarity depend on at least two factors. (a) Frequency of occurrence — how often do forms that are clearly primitive survive to appear in the fossil record long after their more specialized relatives have become extinct? Answering this question completely is impossible until the phylogeny is worked out. Lazarus and Prothero (1984) have suggested, however, that the frequency of such noncorrelation may be high, at least in some groups. (b) Completeness of the record in each case. If the stratigraphic record were perfect everywhere, such noncorrelation could be dealt with by simply examining the stratigraphic distribution of the taxa (Lazarus and Prothero, 1984, p. 166).

Given a stratigraphic record that is not perfect, alternative methods of polarity determination must be sought. Several have been suggested.

"*Reconstruction of the presumed evolutionary pathway*"[35].—Polarity may in some cases be determined by inference from our knowledge of the adaptational history of a group. If a trend seems to be underway in a group (*e.g.*, size increase or a transition from one habitat to another), then the primitiveness of a character state may be inferred by its position in such a transition. Gosliner and Ghiselin (1984) also discuss the use of functional criteria in determining the direction of evolutionary change.

Ontogeny.—Although uncritical application of Haeckel's Biogenetic Law long ago ceased to be a panacea for reconstructing phylogeny, "it is nevertheless true that comparison of (presumably) homologous characteristics of progressively earlier developmental stages of (presumably) phylogenetically related taxa reveals an increasingly general pattern of resemblance among them." (Eldredge, 1979, p. 171) The success with which ontogeny may be used, however, will depend upon the range of variation exhibited in the population (*i.e.*, do they all show the same ontogenetic trend?), as well as the actual evolutionary mechanisms involved (*e.g.*, neoteny *vs.* recapitulation).

Outgroup comparison.—This method is based on the distribution of characters within a monophyletic group compared to that in its sister or outgroup. Wiley (1981,

[35] Mayr, 1981, p. 512; essentially equivalent to "transformation series correlation" of Janvier, 1984, p. 51.

p. 139) gives the following definition of the "outgroup rule": "Given two characters that are homologues and found within a single monophyletic group, the character that is also found in the sister group is the plesiomorphic character whereas the character found only within the monophyletic group is the apomorphic (*i.e.*, derived) character." A method often confused with outgroup comparison is the "commonality principle" (see Watrous and Wheeler, 1981; Schoch, 1986, pp. 134ff), which holds that the character occurring in the most taxa is primitive relative to characters with more restricted distributions. While this principle may correctly indicate polarity in certain cases (primitive features are often shared by sister taxa while derived features are present in only one), these are actually outgroup comparisons. Within single monophyletic groups, selectively advantageous derived characters often occur in the majority of member taxa (*e.g.*, live birth in mammals), making commonality alone of limited value as a polarity indicator.

Ancestor–Descendant Series

Given a pattern of morphological resemblance between two fossil species, two patterns of phylogenetic relationship are possible between an older species **A** and a younger species **B** (Englemann and Wiley, 1977; Bretsky, 1979, pp. 118–119; Eldredge and Cracraft, 1980): either **A** is ancestral to **B** or **A** and **B** are both descended from an unknown common ancestor. The question is whether it is possible to distinguish between these two alternatives. Several authors have maintained that particular ancestral species can never be identified with certainty and that ancestral supraspecific taxa cannot be identified at all because they are non-monophyletic (*sensu* Wiley, 1981), lack defining shared derived characters, and so are "unreal" groups (see Nelson and Platnick, 1981; Patterson, 1981; Forey, 1982; Janvier, 1984; Schoch, 1986, p. 159–168). This criticism is a *theoretical* one; phylogenetic reconstruction at the level of actually specifying who gave rise to whom is held to be impossible in principle.

Even if a number of fossil species are known and their apparent stratigraphic ordering accurately reflects the ordering of the taxa in time, they may not have direct genealogical relationship to each other (Bretsky, 1979, p. 119). This criticism is a *practical* one; reconstruction of phylogeny will be difficult (perhaps even impossible) given an imperfect record.

It is important to make clear here what is really usually meant in practice by the proposition of ancestor–descendant relationships in paleontology. It is indisputable that one cannot ever know with certainty the exact, real order of ancestors and descendants at the species level. Therefore, all that can be hoped for is a successive approximation of where and when ancestral forms existed, and what they may have looked like. This is what is meant when a supraspecific taxon is described as "ancestral". I agree with Bretsky (1979, p. 154; see also Harper, 1976, p. 184) that "expressing an ancestor–descendant relationship between supraspecific taxa of a particular rank symbolized the degree of confidence which one has in a hypothesis about phylogeny . . . ." Specifying that one fossil taxon was ancestral to another is done with a certain degree of uncertainty, but also with a certain degree of confidence that it or some very similar (*i.e.*, closely related) species from about that place and time *was* ancestral. The same idea was expressed by Simpson (1961, pp. 120ff) as the concept of "minimum monophyly" for the inference that, for example, fossil genus **X** is said to be ancestral to fossil genus **Y** when evidence is inadequate for establishing exactly which species of **X** was actually ancestral to the first species of **Y**.

Recanting some of his earlier opinions (*e.g.*, Englemann and Wiley, 1977), Wiley (1981) admits that it is possible to postulate ancestral species, but only when morphological, stratigraphic, and biogeographic data are available to apply to groups with "good" fossil records. Ancestor–descendant hypotheses (*e.g.*, "**A** was the ancestor of **B**") are thus more difficult to assess than sister group hypotheses (*e.g.*, "**A** is more closely related to **B** than to **C**") because more data are needed to confirm the former than the latter.

Phylogenetic Analysis of the *Bullia* Group

Method

Based on the reasoning presented in the previous section, the approach to phylogenetic analysis used here is a combination of cladistic and stratophenetic methods. In broad outline, it follows that advocated by Eldredge (1979) and is divided into three stages:

(a) Morphological characters (listed in Table 15a) have been used to construct and evaluate cladograms. Assumptions of homology are based largely on simple positional criteria, but stratigraphic criteria have also been used where these were apparent and seemed well-supported. Polarity determinations are based on a combination of outgroup comparison and stratigraphic order, with limited application of ontogenetic information. The character matrix given in Table 15b was analyzed using the program **PAUP** (**P**hylogenetic **A**nalysis **U**sing **P**arsimony), version 2.4, written by David Swofford (see description in Fink, 1986). **PAUP** generated a series of most parsimonious trees (cladograms), as measured by the number of character changes required. These cladograms were then analyzed by the

Table 15a.—Morphological characters used for cladistic analysis of taxa in the *Bullia* group.

1. apertural striae
   a. absent
   b. present but faint
   c. present and well-developed
2. apertural lip
   a. internal striae (if present) reflect external spiral sculpture
   b. internal striae (if present) do not reflect external spiral sculpture
3. spire height
   a. ¼ total height (short)
   b. ¼–½ total height (moderate)
   c. ½ total height (elongate)
4. overall development of external sculpture
   a. well-developed
   b. reduced
5. early teleoconch sculpture (axial)
   a. absent
   b. present
6. early teleoconch sculpture (spiral)
   a. absent
   b. present but reduced
   c. present and well-developed
7. late teleoconch sculpture (axial)
   a. absent
   b. present only on posterior half of whorl or less
   c. present over entire whorl
8. axial nodes or spines on late teleoconch whorls
   a. absent
   b. occasionally present
   c. present
9. late teleoconch sculpture (spiral)
   a. absent
   b. present but reduced to only subsutural band and around anterior neck
   c. present but obsolete over middle of body whorl
   d. present over entire body whorl but faint
   e. present and well-developed over entire body whorl
10. terminal columellar fold
    a. absent
    b. present
11. anterior canal
    a. relatively elongate
    b. relatively short
    c. very short
12. posterior notch or slit
    a. absent
    b. occasionally present
    c. present
13. protoconch
    a. small, multispiral
    b. large, paucispiral
    c. large, paucispiral, slightly heterostrophic
14. average total adult height
    a. 20 mm
    b. 20–30 mm
    c. 30–50 mm
    d. >50 mm
15. callus
    a. (if present) extending smoothly over columella and body whorl
    b. (if present) separated from columella by slit and/or ridge
16. callus thickness
    a. reduced or absent
    b. thin
    c. thick
17. columella
    a. smooth on callus
    b. plicate
18. anterior "stromboid-like" notch
    a. absent
    b. occasionally present
    c. present
19. sutures
    a. simple
    b. channeled
    c. enamelled
20. width
    a. ½ total height (elongate)
    b. >½ total height (moderate to squat)
21. recurved siphonal channel
    a. absent
    b. present
22. shouldering
    a. absent
    b. occasionally present
    c. present
23. shell thickness
    a. very thick
    b. thick
    c. thin
24. lateral radular tooth
    a. bicuspidate
    b. multicuspidate
25. foot
    a. very large
    b. not especially large
26. posterior metapodial tentacles
    a. 0
    b. 1
    c. 2
27. eyes
    a. absent
    b. present
28. cephalic tentacles
    a. long
    b. short
29. habit/habitat
    a. deep water
    b. shallow subtidal
    c. subtidal to intertidal
    d. variable

program **CONTREE**, also written by Swofford, which derives a consensus tree summarizing these shortest trees. Programs were run on an IBM-XT personal computer. The resulting consensus tree is discussed in the light of the assumptions of parsimony analysis, the morphological characters used, and their distribution among living and fossil taxa, and justification is given for accepting the preferred cladogram.

(b) The preferred cladogram has been combined with other data to construct a phylogenetic tree for the family Nassariidae. Eldredge (1979), among others, maintains that phylogenetic trees cannot be constructed un-

Table 15b.—Character matrix used for phylogenetic analysis of taxa in the *Bullia* group. Refer to Table 15a for definitions of abbreviations of characters and character states. Character state abbreviations in **boldface** are most commonly expressed; those in *italics* are only occasionally expressed. ? = character state could not be determined. * = character state is ambiguous.

	taxa																					
character	Buccinidae	*"Adinopsis"*	*Buccinopsis*	*Bullia (Buccinanops)*	*Bullia (Bullia)*	*Bullia (Bullia) ? granulosa*	*Bullia (Bullia) ? terebraeformis*	*Bullia (Bulliopsis)*	*Bullia (Cercobullia)*	*Calophos*	*"Cyllenina" 1*	*"Cyllenina" 2*	Cylleninae	*Desorinassa*	*Dorsanum* s. s.	*Keepingia*	*"Molopophorus"*	Nassariinae	*Pseudocominella*	*Thanetinassa*	*Whitecliffia*
1	*ab*c	b	a	a	a	a	a	a	a	*abc*	a	a	*abc*	a	a*b*	a*b*	a*b*	c	*abc*	a	a*b*
2	a	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b
3	b*c*	c	a	a*b*	*abc*	c	c	b	c	b	b*c*	b	b	b	b	b	b	a*b*	a*b*	b	b
4	a*b*	b	a	b	a*b*	b	b	b	a	b	a	a	a	a	b	a	a	a	a	b	b
5	a	b	a	a*b*	a*b*	b	b	a*b*	b	a*b*	a*b*	a*b*	a	a*b*	b	a*b*	b	b	b	b	a*b*
6	c	c	c	a*b*	a*b*	b	b	a*b*	b	*bc*	c	c	a*c*	c	a*b*	c	c	c	c	c	c
7	a*c*	a	*bc*	a*b*	a*b*	b	b	a	c	a*b*	*bc*	*bc*	a*c*	a	a	a*b*	*abc*	a*c*	c	c	a*b*
8	a	a	a	b	a*c*	a	a	a	c	a	a	a	a	a	a	a	a	a	c	a	a
9	a*d*	d	*ce*	d	a*bd*	d	d	a*b*	d	c	e	e	d*e*	a*c*	e	e	d*e*	d*e*	e	e	a*c*
10	a*b*	a*b*	b	b	a*b*	b	b	b	a	b	b	b	b	b	b	b	b	b	b	b	b
11	*abc*	b	a	b	b	b	b	b	b	b	b	b	b	b	b	b	b	c	c	b	b
12	a	a	a	b	a	a	a	a	a	b	c	a	c	a	a	a	a	c	a	c	a
13	b	b	?	b	b	b	a	b	?	b*	a	a	a*	b*	a	c	a*	a*b*	a	?	?
14	c	b	c*d*	c*d*	b*c*	b	b	a*b*	a	a*bc*	b	b	a	a*b*	b	b	b	a	b	a	b
15	a	a*b*	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	a	a	a
16	b	a	b	*bc*	b*c*	a	a	*bc*	a	b	b	b	b	c	b	b	b	b	b	a	c
17	a	a	a	a	a	a	a	a	a	a	a	a	b	a	a	a	a	a	a	a	a
18	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	c	a
19	a	a	a	a*c*	a*c*	a	a	a	a	a	a	a	b	a	a	a	a	a	a	a	a
20	b	a	b	b	a*b*	a	a	b	a	b	b	b	b	b	b	b	b	b	b	a	b
21	a	a	a	a	a	a	a	a*b*	a	a	a	b	a	a	b	b	b	a	b	a	b
22	b	a	c	b	b	a	a	b	a	b	b	b	a	a	a	c	b	b	c	a	b
23	b*c*	c	b	b*c*	b*c*	c	c	c	c	b*c*	b	b	b	c	c	b	b	*ab*	b	b	b
24	b*	b	?	b	b	a	a	?	?	?	?	?	a	?	a	?	?	a	?	?	?
25	b	?	?	a	a	?	?	?	?	?	?	?	b	?	b	?	?	b	?	?	?
26	a	?	?	b	c	?	?	?	?	?	?	?	?	?	a	?	?	*abc*	?	?	?
27	b	b	?	a	a	?	?	?	?	?	?	?	b	?	b	?	?	b	?	?	?
28	b	?	?	a*	a	?	?	?	?	?	?	?	?	?	b	?	?	b	?	?	?
29	d	a*	?	b	b*c*	b	?	b	?	?	?	?	?	?	b*	?	?	b*c*	?	?	?

less the assumption of no character reversal or homoplasy is made. It is clear from the discussion above that such an assumption is not justified for the group discussed here. One can, however, propose hypotheses in the form of trees if ancestor–descendant status can be inferred from stratigraphic and/or geographic position. This is the main technique employed here.

(c) The phylogenetic tree has been placed in a geographic context, and a scenario proposed to describe the biogeographic history of the group. This differs from what Eldredge (1979, p. 168) defines as a "phylogenetic scenario", that is, "a phylogenetic tree with an overlay of adaptational narrative." Emphasis here has been less on the evolution of morphology than on explaining the stratigraphic and geographic distribution of taxa within the group.

Morphological patterns and construction of cladograms are treated in the remainder of this section. The phylogenetic tree and biogeographic scenario are discussed together in the conclusion (pp. 110–115).

Outgroup Comparison

Eldredge (1979, p. 171) has emphasized that there is no hard and fast rule governing the selection of the correct outgroup for comparison with the taxon of interest. Outgroup comparison should rather be viewed as a continuous procedure of pair-wise comparison.

Potential sister groups are proposed on the basis of previous or independent phylogenetic information and analysis, and alternatives are tested by how well they accord with all available data. In the case of the *Bullia* group, there are a number of groups that could conceivably be the sister group (*e.g.*, buccinids, other nassariids). As discussed on pp. 9–12, however, the interrelationships of these groups are insufficiently known to allow one to be specified as the closest relative to the *Bullia* group.

In the absence of detailed systematic revision of the varied buccinoid groups, and of a consensus on the interrelationships of nassariid subfamilial groupings, it is impossible to make precise outgroup comparisons. I have, therefore, tended to frame outgroups very broadly at higher taxonomic levels. In the **PAUP** analyses, I have defined Buccinidae s. l. as the outgroup for Nassariidae. In the discussion below I use nassariines and cyllenines together as an outgroup for the *Bullia* group. Within the *Bullia* group itself, relationships are not clear enough *a priori* for any real advantage to be gained by proposing specific outgroups, and other methods are used.

Morphological Analysis

Using Buccinidae s. l. as an outgroup for Nassariidae suggests that relatively short spire, elongate anterior canal, pronounced external sculpture, nonplanktotrophic development, and a maximum adult total height of approximately 30 mm are all primitive with respect to nassariids. The following conchological characters are shared by most or all members of Nassariidae (see Pl. 1), and allow it to be recognized as a monophyletic group:

(1) terminal columellar fold, varying from simple to complex. As mentioned on p. 10, it is possible that this variation in the form of the anterior end of the columella indicates that not all folds are homologous. A more detailed examination will be required to confirm their homology. A terminal columellar fold is present in all nassariids except some Recent species of *Bullia* s. s.

(2) In those nassariids that have spiral sculpture on both the inside and outside of the shell, the patterns on the inside and outside do not correspond, as in most species of buccinids (s. l.).

(3) In overall shell form, nassariid species are distinct. The spire very seldom comprises more than one-half the total height, and the whorls of the spire are not usually notably inflated. The anterior canal is usually relatively short, and the aperture usually relatively small.

Based on several methods of polarity analysis, axial and spiral shell sculpture seem to be primitive relative to a smooth shell. Conspicuous axial and spiral sculpture are widespread in Nassariinae, Cylleninae and many buccinoids (see *e.g.*, Text-fig. 2; Pl. 1, figs. 1–3, 9). Several species of *Calophos* Woodring, 1964, *Buccinanops* d'Orbigny, 1841, and some individuals of *Dorsanum miran* (Bruguière, 1789) show sculptural elements on the early teleoconch which become obsolete on adult whorls. If *Buccinopsis* Conrad, 1857 is seen as an ancestral taxon for any or all nassariids, then pronounced axial and spiral sculpture are primitive by stratigraphic criteria. It is interesting to note, however, that at least one species of *Buccinopsis* [*B. dorothiella* Sohl, 1964] shows a pattern of sculpture similar to that in several later *Bullia* group taxa, in which both axial and spiral sculpture become obsolete on the middle of the body whorl.

By general outgroup comparison, the presence of striae inside the outer lip of the aperture would seem to be primitive relative to a smooth interior. The distribution of this character among taxa is complex, however, and it is probably not homologous in all taxa. Most species of Nassariinae, Cylleninae and Buccinidae show grooves and/or ridges inside the aperture (Text-fig. 2; Pl. 1, figs. 1–3, 9). *Buccinopsis* does not, however, show any striations or ribbing in the aperture. Whatever the homologies, on stratigraphic grounds there appears to have been a general reduction in all types of apertural striae throughout the history of the group.

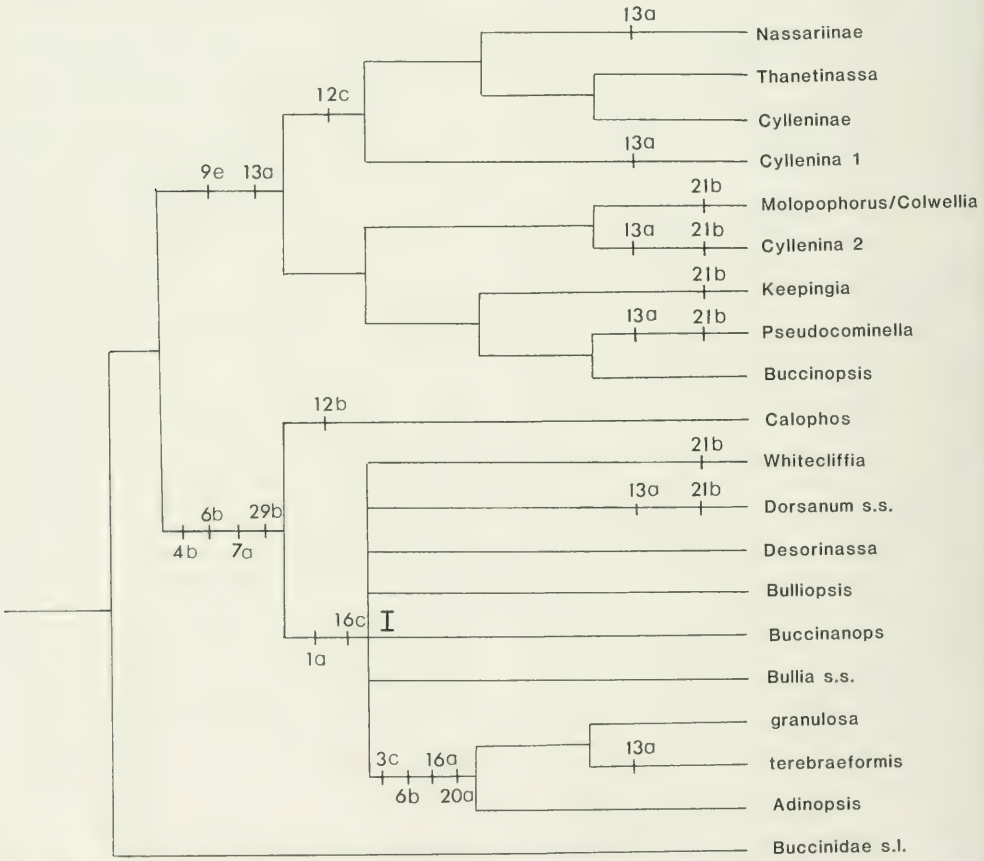
Planktotrophy is probably primitive in neogastropods (Jablonski and Lutz, 1983, p. 57), and there has probably been a continuous increase in the proportion of nonplanktotrophic species within the group since the Cretaceous. Some nonplanktotrophic taxa, however, may have sufficient evolutionary flexibility to reacquire a planktotrophic habit due to their retention of larval feeding structures (Strathmann, 1978, p. 901). All living species in Buccinidae s. l. are nonplanktotrophic (Radwin and Chamberlain, 1973; Ponder, 1973; Robertson, 1974). It is, therefore, possible that nonplanktotrophic development, although derived with reference to Neogastropoda as a whole, is the primitive condition in Nassariidae, and that in a few taxa (*Dorsanum* s. s., *Pseudocominella* Nuttall and Cooper, 1973, some European "*Cyllenina*" species, and some living species of *Nassarius* Duméril, 1806) planktotrophic, or at least planktonic, development arose as a derived condition.

As most buccinids and almost all nassariines have eyes, it is reasonable to assume that this is the primitive condition. The foot of most species of Nassariinae bears two posterior metapodial tentacles, although some have only a single tentacle or none at all (Cernohorsky, 1984, p. 32; personal observations). Most buccinids lack such tentacles, suggesting that absence is the primitive condition at the family level. If this is the case, then *Bullia*

s. s. and some nassariines show the derived condition, while other nassariines and *Buccinanops* are intermediate; *Dorsanum miran* (Bruguière, 1789) would then be seen as retaining the primitive condition.

PAUP produced 13 different shortest (equally parsimonious) cladograms of length 94. The strict consensus tree (**SCT**, see, *e.g.*, Marshall, 1986) was determined by **CONTREE** following the method of Rohlf (1982), and is given in Text-figure 24.

The most conspicuous aspect of the **SCT** is the low level of resolution at the node labeled "**I**". Inspection of the 13 individual cladograms summarized by the **SCT** shows that the characters involved in this node include external sculpture (characters 5–7, 9), subsutural shouldering (character 22), shell thickness (character 16), and callus thickness (character 23). Table 15b shows that these characters are among the most polymorphic characters in the analysis; that is, different species or individuals within the taxa treated show more than a single character state. Almost 13% of the 609 total possible character-taxon combinations (or more than 15% of the combinations with known values) are polymorphic. Since **PAUP** 2.4 cannot deal with polymorphism directly, it was either coded into the list of character states (*e.g.*, characters 12, 18, 22) or ignored in the analysis. In the latter cases the state used for each character was that most commonly expressed. For example, not all species of *Bullia* s. s. lack



Text-figure 24.—Strict consensus tree (SCT) derived from 13 most parsimonious cladograms generated by PAUP from the character matrix given in Table 15b. Indicated near the base of the cladogram are the major character state transitions controlling tree topology. On the branches to the right are shown the distribution of recurved siphonal channel (character 21) and protoconch form (character 13).

a terminal columellar fold [*e.g.*, *B. annulata* (Lamarck, 1816a)], but the great majority do, and so character 10 was listed as "absent" for this taxon.

Much of the lack of resolution at node "**I**", therefore, is probably due to the ambiguous nature of the size, shape, and sculptural characters that comprise much of the data set. Other Recent gastropods are known to be variable in expression of external sculpture (see, *e.g.*, Struhsaker, 1968; Palmer, 1984), within genera and even species, responding to both genetic and environmental factors. At the same time, however, it is clear that certain supraspecific taxa show greater overall development of external sculpture than others. As already mentioned, on the basis of outgroup comparison and stratigraphic order, external sculpture appears to show an overall trend toward reduction within the *Bullia* group. In Nassariidae it thus seems reasonable to infer that well-developed external sculpture is primitive relative to less pronounced sculpture, but to avoid relying too heavily on external sculpture as a criterion for inferring branching order.

The importance of the recurved siphonal channel around the anterior end of the fasciole (character 21 in Tables 15a, b) is probably not adequately reflected in the **SCT** arrangement of taxa given on the cladogram in Text-figure 24. The **SCT** includes *Dorsanum* s. s. and *Whitecliffia* Nuttall and Cooper, 1973 in the poorly resolved group above node "**I**" with *Bullia* s. s., *Buccinanops*, *Bulliopsis*, *Desorinassa* Nuttall and Cooper, 1973, *Adinopsis* and the two problematic living species *terebraeformis* and *granulosa*, and separates them, mainly on the basis of sculptural characters, from the other taxa (*Pseudocominella*, *Keepingia* Nuttall and Cooper, 1973, "*Cyllenina*" 2, "*Molopophorus*") that show this feature. As displayed by these taxa, the recurved siphonal channel is a distinct, relatively complex and readily recognizable shell character. With the exception of the slightly different channel showed by several specimens of Eocene *Bulliopsis*, no supraspecific taxon is polymorphic for this character. For reasons discussed on pp. 55, 56, the channels showed by these *Bulliopsis* specimens do not appear to be homologous with those of these six taxa.

Acceptance of a grouping based on the recurved siphonal channel would mean that the smooth form of species of *Whitecliffia* and *Dorsanum* s. s. arose independently from that in species of *Bullia* s. s., *Buccinanops*, and *Desorinassa*. As Marshall (1986, p. 160) summarized a similar problem, the choice between the two can be reduced to whether the recurved siphonal channel is more or less likely to have evolved by homoplasy than aspects of external sculpture. If more likely, the **SCT** is to be favored; if less likely, another arrangement should be proposed.

An alternative cladogram is given in Text-figure 25. It accepts and uses many of the relationships shown in the **SCT**, but differs in other aspects. I prefer this cladogram for at least five reasons.

First is the high probability of homoplasy in general in gastropod shell form, making it unlikely *a priori* that simple acceptance of a most parsimonious tree will yield the correct phylogeny.

Second is the evidence favoring the weighting of certain shell characters over others. General shape, size and external sculpture are the aspects of gastropod shell form most often employed in paleontological analyses. These characters, however, are probably also the most prone to homoplasy, and so are least reliable for phylogenetic inference. Clearly recognizable, distinct, and complex features such as the terminal columellar fold and recurved siphonal channel are more likely to be homologous, and so should be given more attention in choosing cladistic patterns.

Third, acceptance of the **SCT** would imply either that *Buccinopsis* lost the recurved siphonal channel or that it arose two or more times among "*Molopophorus*", "*Cyllenina*" 2, *Keepingia*, and *Pseudocominella*. The first hypothesis appears unlikely on stratigraphic criteria; if *Buccinopsis* represents the ancestral condition for Nassariidae, absence of a recurved siphonal channel is primitive. The second appears unlikely for the reasons already given that support the hypothesis of homology of the recurved siphonal channel in various groups.

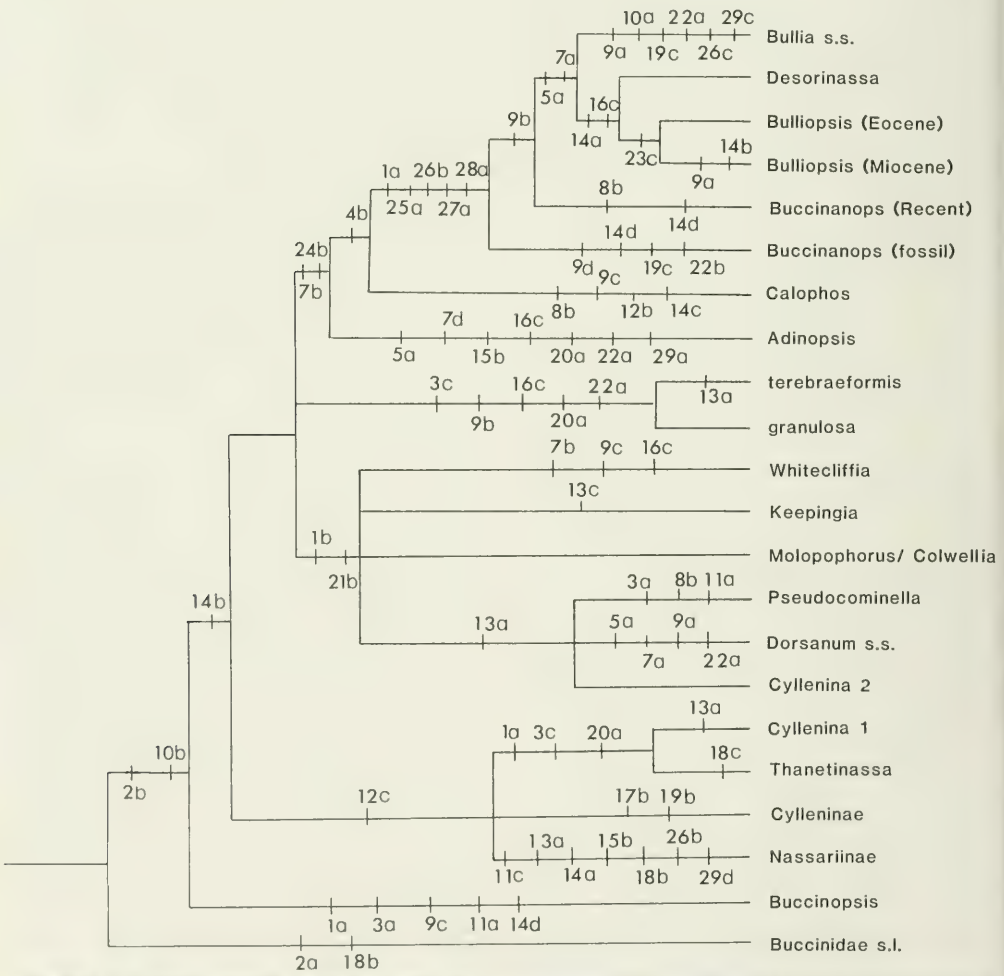
Fourth, an arrangement of taxa based on the presence/absence of a recurved siphonal channel is supported to some degree by the distribution of protoconch and radula form. *Dorsanum* s. s., *Pseudocominella*, "*Cyllenina*" 2, and probably *Colwellia* Nuttall and Cooper, 1973 all show small multispiral protoconchs. The protoconchs of *Whitecliffia* and most species of *Molopophorus* are unknown. Similarly, *Desorinassa*, *Bulliopsis*, most species of *Bullia* s. s., *Buccinanops*, and perhaps *Calophos* all show large, paucispiral protoconchs. As discussed on p. 14, the radular form of *Dorsanum* s. s. differs from that of *Bullia* s. s., *Buccinanops*, and *Adinopsis* Odhner, 1923.

Fifth and finally, the diversity of fossil forms showing a recurved siphonal channel is persuasive. If only Recent taxa (*Dorsanum* s. s., *Bullia* s. s., *Buccinanops*, and "*Adinopsis*") were known, it would be more difficult to argue for a very old and basic phylogenetic subdivision among them. The existence of so many fossil species bearing a distinctive morphological feature shown among living forms only by *Dorsanum* s. s., however, suggests that this feature arose early in the history of the group, and that more than a single lineage is represented by the Recent species.

A more detailed consideration of the relationships posited in Text-figure 25 follows.

The phylogenetic position of *Cyllene* Gray, 1834 is based on its sharing with species of Nassariinae a marked posterior notch, complex fasciole, and well-developed spiral and axial sculpture. Species of *Cyllene* are relatively more elongate, especially in the anterior portion of the columella, where unlike most species of *Nassarius*, the callus passes smoothly onto the columella and body whorl. The apertures of species of *Cyllene* are relatively larger than in most nassariines, and they show a somewhat broader range of sculptural types (see Cernohorsky, 1984).

Some European Tertiary species referred to here as "*Cyllenina*" 1 share with *Thanetinassa* Nuttall and Cooper, 1973 the importance of tubercular sculpture and relatively high spires. If these are grouped together, it is assumed that their axial–tubercular sculpture is homologous, but there is no definite evidence for this beyond simple positional similarity. Both show well-



Text-figure 25.—Preferred cladogram for the family Nassariidae, with distribution of all relevant character transformations. Not shown for lack of space are the characters shared by all taxa (nassariids and outgroup Buccinidae s. l.), which are as follows: 1c, 3b, 4a, 5b, 6c, 7c, 9e, 11b, 13b, 14c, 15a, 16b, 17a, 18a, 19a, 20b, 21a, 22b, 23b, 26a, 29b.

developed posterior slits or notches in the apertures, and on this basis are grouped with Nassariinae and Cylleninae. *Thanetinassa* is unique in Nassariidae in its possession of a "stromboid-like" notch at the anterior end of its aperture (Nuttall and Cooper, 1973).

The remainder of Nassariidae comprises the "*Bullia* group". No morphological character unites these taxa to form a demonstrably monophyletic group, and although monophyletic clades are recognizable within it, their branching order is obscure. Two main subgroups are distinguishable. One is defined by the possession of the recurved siphonal channel on the dorsal anterior portion of the fasciole. No other definite shared derived characters can be identified as corroborating this grouping. *Pseudocominella* is the distinguished from the others among this set by its elongate siphonal canal, shorter spire, and pronounced axial sculpture. In these characters, *Pseudocominella* resembles *Buccinopsis*, and so may be the most primitive member of its lineage. This is reflected by its position in the **SCT** (Text-fig. 24).

Some species of "*Cyllenina*" ("*Cyllenina*" 2) from the European Tertiary also bear a reflexed siphonal channel bounded by carinae. The external sculpture and overall shape is variable in these species (see Pl. 13, fig. 7). Nuttall (written commun., 1985) believes that some European fossil species previously assigned to *Dorsanum* Gray, 1847 are the direct ancestors of living *D. miran* (Bruguière, 1789). These species bearing the siphonal channel may represent such an ancestral group.

It seems doubtful that all seven "*Molopophorus*" species tentatively suggested as related to the *Bullia* group belong to a single supraspecific taxon (see, *e.g.*, Vokes, 1939; Hickman, 1969, p. 90). Some or all may be able to be incorporated into the genus *Colwellia*. These species share with *Dorsanum miran* (Bruguière, 1789) and *Pseudocominella* the reflected anterior siphonal channel on the fasciole. Sculpture in these West Coast species ranges from a somewhat cancellate pattern, with the axial elements predominating [*e.g.*, *M. anglonanus* (Anderson, 1905)], to axial sculpture only [*e.g.*, *Colwellia bretzi* (Weaver, 1912)], to nearly smooth [*e.g.*, "*M.*" *bogachielii* (Reagan, 1909)]. It is not possible at present to suggest characters that discriminate between *Colwellia* and these species assigned to "*Molopophorus*", if indeed such characters exist, and these two taxa are treated together.

The genus *Keepingia* is a heterogeneous one, sharing with *Colwellia*/"*Molopophorus*", *Pseudocominella*, and *Dorsanum* s. s. a reflexed siphonal channel on the fasciole. From the published figures of Nuttall and Cooper (1973), it appears that some species have striae on the inside of the outer apertural lip, while others do not. External sculpture is variable, in some specimens resembling *Cyllene*, in others *Colwellia*, and others *Pseudocominella*. Nuttall and Cooper suggest that *Keepingia* most closely resembles *Colwellia*, differing most importantly in the form of its protoconch, which is slightly heterostrophic.

On the cladogram in Text-figure 25, the branching order of "*Molopophorus*"/*Colwellia*, *Keepingia*, and *Whitecliffia* is unresolved, reflecting their close morphological similarity. Their phylogenetic relationships to each other must be close, but the details remain unknown. Stratigraphic ordering is of little help here (Text-figs. 1, 21).

The phylogenetic relationships of *Bullia* ? *granulosa* (Lamarck, 1822) and *Bullia* ? *terebraeformis* (Dautzenberg, 1913) are difficult to discern. They share the form of the lateral radular tooth with living *Dorsanum miran* (Bruguière, 1789), but do not bear the reflexed siphonal channel. They are similar to each other in their lack of parietal callus, relatively simple apertures, and high spires, and to some degree in their external sculpture (which is actually similar to that of some species of *Bullia* s. s.). They differ from each other, however, in the form of their protoconchs, that of *terebraeformis* being small and multispiral and that of *granulosa* being large and paucispiral (Adam and Knudsen, 1984). It may be misleading to continue to argue over the assignment of these species to either *Dorsanum* s. s. or *Bullia* s. s. Although definitive evidence is clearly lacking at present, they may belong to a lineage separate from both living genera.

"*Adinopsis*" *skoogi* Odhner, 1923 similarly resists assignment to either living *Bullia* s. s. or *Dorsanum* s. s. It shares with *Bullia* a multicusp lateral radular tooth, lack of pronounced axial sculpture, and a large paucispiral protoconch. It is distinct in its very reduced parietal callus and the presence of spiral sculpture over the entire shell. The **SCT** (Text-fig. 24) links "*Adinopsis*" with *Bullia* ? *terebraeformis* and *B.* ? *granulosa*, largely on the basis of elongate shape and reduction of callus and sculpture. The radula of "*A.*" *skoogi*, however, agrees more closely with those of species of *Bullia*, while the radulae of *terebraeformis* and *granulosa* resemble that of *Dorsanum miran*. Other characters should be sought to resolve these conflicting patterns.

The second large distinguishable group within the "*Bullia* group" includes those forms that most closely resemble *Bullia* s. s. in overall shell form. The genus *Calophos* is distinguished by the following combination of characters: (1) spire comprises one-third to one-half total height; (2) body whorl relatively inflated; (3) striae on inside of outer apertural lip; (4) spiral sculpture always present, but usually only on spire whorls and subsutural and anterior portions of the body whorl;

obsolete over middle one-half to one-third of body whorl; (5) axial sculpture often present on early teleoconch and sometimes on body whorl — always widely spaced, faint and blunt on body whorl.

These are all, however, primitive characters. *Calophos* is here recognized as a group of similar species showing these characters and lacking others. Such a grouping does not follow strict cladistic methods, under which the group would have to be represented by an unresolved polychotomy of species and could not be classified as a single, genus-level taxon. The species assigned here to *Calophos*, however, appear to comprise a morphologically, chronologically, and geographically coherent group, representing a stage of evolution in the *Bullia* group as a whole. This is the explicit justification for the recognition of the genus.

As already mentioned, the European Miocene species *Nassa veneris* Faujas de Saint-Fond, 1817 is very similar to some species of *Calophos* [*e.g. C. plicatilis* (Böse, 1906); see Pl. 12, figs. 13, 15]. Cossmann (1901b, p. 219) noted that *veneris* was distinct from other forms from the European Tertiary that he assigned to *Dorsanum*. It is larger, the conspicuous beaded sculpture characteristic of the other species is lacking or greatly reduced, and the fasciole lacks any recurved siphonal channel. It shares with *Calophos* a similar overall shape and size, predominance of moderate spiral sculpture, slight shouldering, internal spiral sculpture in most individuals, and a simple, relatively short columella bearing a terminal columellar fold. The protoconch of *N. veneris* is small and multispiral, similar to those of other forms assigned to *Dorsanum* from the European Tertiary (see Pl. 14, figs. 1–6). The known protoconchs of *Calophos* species (one species from Florida and one species from Panama), in contrast, are relatively large (see further discussion below [p. 112]).

As in *Calophos*, the species of *Desorinassa*, *Buccinanops*, *Bulliopsis*, and *Bullia* s. s. do not exhibit discrete, clearly nested sets of characters allowing strict cladistic analysis. As a group, however, they are characterized by the following conchological characters:

(1) No species show axial sculpture on later whorls of the teleoconch, although it may be present on the earliest whorls [*e.g.*, in *Buccinanops cochlidium* (Dillwyn, 1817)].

(2) When present, spiral sculpture is reduced even further from its expression in most species of *Calophos*, occurring either as faint grooves just below the suture and around the fasciole or as very faint grooves over the whole of the whorls, being even fainter across the middle. Some species show no sculpture whatsoever, and others only subsutural bands of one or two spiral grooves or ridges.

(3) Similar overall form. The spire comprises one-third to one-fourth the total height (except in some species of *Bullia* s. s.; see discussion on p. 17); the aperture usually comprises approximately one-half the total height; the profile of the whorls is usually rounded, with the exception of shouldering shown by some forms. A terminal columellar fold is present and simple (except in most species of *Bullia* s. s.).

(4) All lack internal sculpture.

(5) All have a relatively thick and/or expanded parietal callus.

Fossils from southern South America and Antarctica described on pp. 79–82 [*Buccinanops fuegina* (Steinmann and Wilckens, 1908), *B. nordenskjoldi* (Steinmann and Wilckens, 1908)] appear to represent the transition between more sculptured forms (represented by *Calophos*) and smoother forms (represented by living species of *Buccinanops* and *Bullia* s. s.). The body whorl of these fossil species has a smooth rounded profile but bears spiral grooves over most or all of the surface. In Recent species of *Buccinanops*, external sculpture is very reduced, the exceptions being the spines of *B. moniliferum* (Kiener, 1834) and the polymorphic shouldering of *B. cochlidium* (Dillwyn, 1817). This is reflected in the cladogram in Text-figure 23 by the separation of fossil from Recent forms of *Buccinanops*. Similar heterogeneity, discussed on pp. 53–56, is evident when Miocene and Eocene species of *Bulliopsis* are discriminated cladistically. Trends toward increased size and decreased external sculpture, already discussed, are clearly shown.

Similarities between Early Tertiary European species assigned to *Desorinassa* and Eocene forms from the southeastern U. S. assignable to *Bulliopsis* have already been discussed. The type species of *Desorinassa*, *D. desori* (Deshayes, 1865), agrees particularly well with *B. choctavensis* (Aldrich, 1886). They are of similar size and both have spiral external sculpture restricted to a subsutural collar and around the anterior neck region of the body whorl. Other species assigned by Nuttall and Cooper (1973) to *Desorinassa* are more similar to the Miocene species of *Bulliopsis* treated on pp. 29–53. It is clear that *Desorinassa* is very closely related to *Bulliopsis*. If they occurred on the same side of the Atlantic it would probably be reasonable to unite them in a single supraspecific taxon.

As discussed on pp. 12, 13, *Bullia* s. s. is today a relatively specialized animal ecologically, modified in its shell, body form, and physiology to take full advantage of life in the high-energy intertidal zone of sandy shores. Many physiological and soft part characters of these gastropods seem to be modifications for this habitat, and it may be reasonable to explain some of *Bullia*'s conchological characteristics in a similar manner. The loss of the terminal columellar fold as well as the almost total absence of sculpture on the majority of species may be morphological conse-

quences of life in the sandy intertidal zone. It may be significant that the oldest fossil representative of *Bullia* s. s. [*B. annulata* (Lamarck, 1816a), as *B. magna* Haughton, 1932] shows both the terminal fold and well-developed spiral sculpture (see Pl. 2, fig. 4).

PALEOBIOGEOGRAPHIC FRAMEWORK

Biogeographic patterns, as revealed by physical and biological evidence, serve as both framework and constraint for the construction of phylogenetic hypotheses. This is especially important in a widespread and diverse taxonomic group. The evolution of the *Bullia* group took place among moving continents, separated by thousands of kilometers, around which sea levels were rising and falling. Its lineages were but a very few of the countless others that migrated, evolved, and became extinct with these changing physical conditions. An understanding of these biotic and abiotic factors shapes and limits our choice of scenarios for the evolution of these organisms, and is an important component in the information necessary to derive acceptable phylogenetic trees from cladograms. From a consideration of plate movements and faunal relationships, detailed in the *Appendix*, it is possible to place a phylogenetic analysis of the *Bullia* group in geographic context.

The geological and paleontological data summarized in the *Appendix* lead to the following conclusions:

(1) Exchange of benthic and pelagic taxa occurred in both directions across the Atlantic throughout the Late Mesozoic and Paleogene. For benthic species, this exchange could have taken place: (a) directly between eastern South America and West Africa until their separation in the Late Cretaceous; (b) along continuous shallow shelf between North America and northwestern Europe until their final separation in the late Eocene; (c) by something resembling a "sweepstakes route" (see, *e.g.*, Simpson, 1940) over the islands of the Río Grande Rise–Walvis Ridge until perhaps as late as the Paleocene; or (d) by mechanisms of long-distance dispersal such as rafting on vegetation. For pelagic species, or benthic species with planktonic dispersal phases, exchange could have and still does occur by long-distance transport *via* ocean currents (Scheltema, 1978, 1979). In the Cretaceous and Early Tertiary, ocean currents in the widening Atlantic apparently favored dispersal from east to west, thus allowing transport of Tethyan and European forms to the Americas (Dilley, 1971, 1973; Luyendyk, Forsyth, and Phillips, 1972; Gordon, 1973; Scheltema, 1979; Cool, 1982). In the later Tertiary, pelagic dispersal may have been easier from west to east (Adams, 1967; Berggren and Hollister, 1974; Briggs, 1974, pp. 109–110). This change could have been associated with the initiation of modern oceanic circulation patterns in the North Atlantic (Berggren and Hollister, 1974; Pinet and Popenoe, 1985).

(2) It is possible that, during at least part of the Early Tertiary, two or more biotic provinces were present in the North Atlantic. One seems to have included the southeastern and eastern coasts of North America, probably West Greenland, and parts of northwestern Europe, and may be referred to as a Euramerican province. The faunas of northwestern Europe during this period may have been heterogeneous and influenced by those of several regions. The other province may have included much or most of the West Indies, as they existed in the Paleogene, at least parts of Florida and the northern coast of South America, and the narrowing Tethyan Ocean between North Africa and southern Europe, and may be called a West Tethyan province. Paleogene faunas of the West Coast of North America show similarities with the faunas of both provinces, and it seems likely that some mixing occurred in this region. These patterns, perhaps never very strong, began to break down in the late Paleogene and Neogene as the Atlantic reached its modern proportions and modern climatic gradients began to be established.

It is possible but as yet unconfirmed that these two provinces were delineated by temperature differences, the Euramerican province being slightly cooler and the West Tethyan warmer and more typically tropical. A combination of temperature and hydrographic effects may have been responsible for a relatively sharp discontinuity between the primarily clastic facies of the American coastal plains and the primarily carbonate facies of Florida and much of the Caribbean (Pinet and Popenoe, 1985). Adjacent but distinct provinces exist in Recent oceans, bounded by steep temperature gradients and have been distinguished in the fossil record (*e.g.*, Hall, 1964; Hecht, 1969; Hazel, 1970; Stanley, 1986). As in modern provinces, these Early Tertiary provinces shared many taxa, and are distinguishable only on the basis of overall patterns of distribution, especially of benthic foraminifera and mollusks.

(3) North–south exchange seems to have been easier in the western Atlantic than in the east. Caribbean and North American faunas have more readily expanded along the coasts of South America than have European faunas along the west coast of Africa. Berggren and Hollister (1974, p. 133) have pointed out, however, that some warm-water species apparently moved south from the Mediterranean region seeking warmer-water refuges along the West African coast in the Neogene. The details and extent of this type of movement are presently unknown.

(4) Large-scale biogeographic studies of Tertiary mollusks are badly needed before these ideas can be supported or rejected with confidence.

DISCUSSION AND CONCLUSIONS

Construction of a phylogenetic tree is, according to Eldredge (1979), a matter of specifying a taxon for every node of the accepted cladogram. "That taxon may be either one of the two taxa at the terminal points of the clades or a third taxon either present as the sister group of [both taxa] or as yet unknown" (Eldredge, 1979, p. 184). The major difficulty in constructing phylogenetic trees is that in almost no cases are all the taxa of interest known. While the ideal phylogenetic tree is an evolutionary "event-o-gram" (Eldredge, 1979, p. 185), in practice such trees are no more than best guesses about what happened when, given the limitations of the record at hand.

In proposing a phylogenetic tree for the family Nassariidae (Text-fig. 1), I have accepted to a large degree the results of the foregoing cladistic analysis. I have also, however, allowed stratigraphic and geographic information to influence the proposition of particular ancestor–descendant relationships.

The evolutionary relationships expressed in Text-figure 1 are presented in an explicitly temporal–geographic context on the paleogeographic maps in Text-figures 26–29. These show the approximate distribution of land and deep and shallow seas over the last 80 million years, and the major hypothesized dispersal events in the history of the *Bullia* group. In this section I summarize these biogeographic and evolutionary events, in the context of a series of ancestor–descendant hypotheses. Poorly constrained aspects of this scenario are highlighted. Although it is undeniable that such a series of postulated events represents a step further away from the actual morphological data of the organisms themselves (see, *e.g.*, Eldredge, 1979; Wiley, 1981), other types of data, such as geographic and stratigraphic distributions, ensure that this scenario is empirically based and that its essential claims and hypotheses are fully testable.

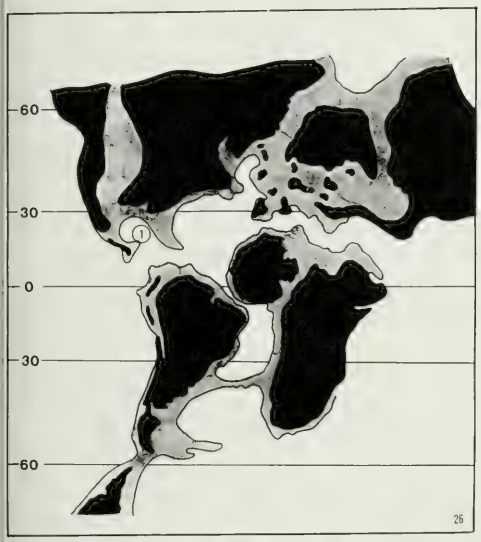
Buccinopsis Conrad, 1857 is the oldest currently recognized gastropod taxon believed to belong to Nassariidae, and the only known pre-Cenozoic representative of the family. Sohl (1964) has summarized the known Late Cretaceous gastropod faunas worldwide, and does not report any form resembling *Buccinopsis* from anywhere outside the U. S. Gulf Coast. *Buccinopsis* agrees well with the conception of the primitive nassariid based on general outgroup comparison, as discussed on pp. 52, 53, and may approximate an ancestor for the family. Given the present state of knowledge, it is also reasonable to suggest that, whatever the ultimate origin of *Buccinopsis* (Sohl's account indicates that this might have been as far away as South Africa or India), post-Cretaceous nassariids may have arisen on the coastal plains of southeastern North America. It should be emphasized that if *Buccinopsis* does not approximate in time and space the first nassariid, then although the sequence of biogeographic events described here may be altered, the basic structure of probable phylogenetic relationships is not. Transatlantic dispersal events are required to explain the Tertiary history of this group. Whether they occurred initially from west to east, as suggested here, or from east to west, must be decided by future work.

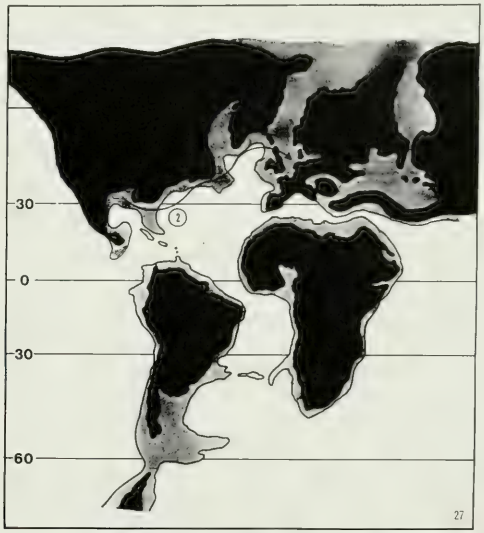
From a *Buccinopsis*-like ancestor in the southeastern U. S., two lineages appear to have evolved initially. One led to the currently most diverse nassariid groups, Nassariinae and Cylleninae. Some Early to Middle Tertiary European forms, including *Thanetinassa* Nuttall and Cooper, 1973 and species referred to herein as "*Cyllenina*" 1 may be related to this lineage. Given the fossil record of nassariines, these events probably occurred in the Old World (see Cernohorsky, 1984). It remains to be investigated whether one or more taxa usually assigned to Buccinidae s. l. (*e.g.*, *Phos* Montfort, 1810) is related to or originated from some member of this group.

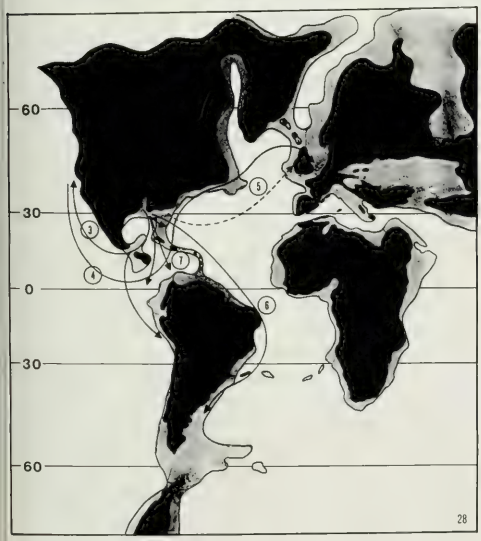
The other lineage comprises the *Bullia* group, which itself split sometime in the Paleocene to form two main subgroups. The first consists of those species bearing

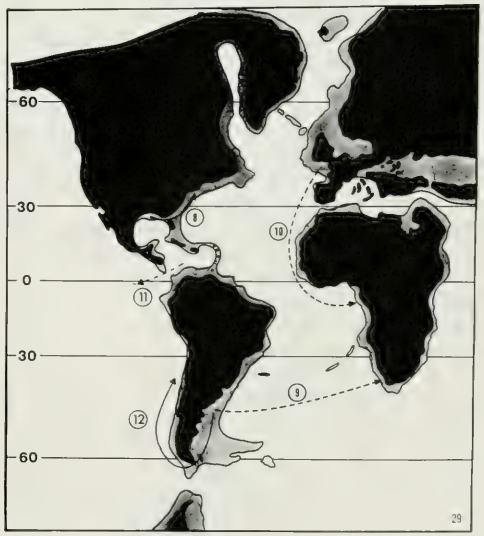
Text-figures 26–29.—Paleogeographic maps of the circum-Atlantic region for the Late Cretaceous to Recent, showing hypothesized dispersal events in the history of the *Bullia* group. These are new maps, synthesized from those of Barron *et al.* (1981), Ziegler, Scotese, and Barrett (1982), Smith and Briden (1977), Sclater, Hellinger, and Tapscott (1977), Rögl and Steininger (1983), and Reyment (1980) to show not only continental position, but also the distribution of dry land (dark shading), shallow marine shelf (light shading), and deep sea (unshaded). **26**, Late Cretaceous, ~80 mya. **27**, Paleocene–Eocene, ~60 mya. **28**, late Eocene, ~40 mya. **29**, Miocene–Pliocene, 10–20 mya. Solid lines indicate inferred benthic dispersal along shallow shelves; dashed lines indicate inferred pelagic dispersal across open ocean. (1) Hypothesized origin of Nassariidae in the Gulf coastal plain area in the Late Cretaceous; (2) benthic dispersal of an ancestor of *Desorinassa*, probably derived from Paleocene representatives of *Bulliopsis*; (3) dispersal of the ancestor of Peruvian Eocene species assigned to *Dorsanum* by Olsson ("*Dorsanum*" *parinense* and "*Dorsanum*" *lagunitense*) from southern North America, and dispersal of descendants of Peruvian or other related North American forms to the west coast of North America to become the *Colwellia* / "*Molopophorus*" group; (4) dispersal of *Colwellia* from western North America to western Europe (mode of dispersal unknown); (5) planktonic dispersal of an ancestor of *Pseudocominella*, "*Cyllenina*" 2, and living *Dorsanum* s. s. from southern North America to western Europe; (6) origin and dispersal of *Buccinanops* from southeastern North America to South America and Antarctica; (7) radiation of the genus *Calophos* in the Caribbean basin; (8) migration of *Bulliopsis* from the Gulf or the Atlantic coast area prior to the middle Miocene; (9) chance dispersal across the South Atlantic of the ancestor of living species of *Bullia* (*Bullia*) in the latest Miocene or early Pliocene; (10) dispersal of the ancestor of Recent *Dorsanum* (probably a form close to those referred to here as "*Cyllenina*" 2) from central or western Europe to western Africa; (11) spread of at least one species of *Calophos* to the Galapagos Islands in late Pliocene; (12) gradual northward expansion of at least one or two species of *Buccinanops* along the western coast of South America.

the carina-bounded, reflexed siphonal channel, and may for the moment be referred to informally as the "*Dorsanum* subgroup". Sometime during the Paleocene, this subgroup gave rise to two lineages. One dispersed, probably by planktonic larvae, from North America to western Europe, and gave rise to species included in *Pseudocominella* Nuttall and Cooper, 1973. *Pseudocominella* or, more likely, another unknown form, was ancestral to the Middle Tertiary European species of "*Cyllenina*" 2, and it was from this complex that living *Dorsanum miran* (Bruguière, 1789) most likely evolved in the Late Tertiary, dispersing southward to western Africa as this continent made contact with southern Europe. The second lineage gave rise to New World forms, including the Peruvian Eocene forms ["*D.*" *parinense* (Olsson, 1928) and "*D.*" *lagunitense*









(Woods, 1922)] and at least some West Coast Middle Tertiary species currently assigned to *Molopophorus* Gabb, 1869 and *Colwellia* Nuttall and Cooper, 1973. A dispersal event to Europe occurred from this stock, giving rise to the species included in *Keepingia* Nuttall and Cooper, 1973 and *Whitecliffia* Nuttall and Cooper, 1973.

This ancestor may have been a species of *Colwellia*. Species so far assigned to this genus occur first in beds of Lutetian age in California, appearing soon afterward in the Auversian and Priabonian of France and England, respectively. Whether this indicates that the group actually arose in the Americas and spread to Europe can only be tested by searching for pre-Auversian representatives in Europe. This interpretation would seem to be supported circumstantially, however, by the high diversity of the "*Molopophorus*" group in the New World. The "*Molopophorus*" lineage may have spread beyond North America around the northern margin of the Pacific; this remains to be confirmed.

The second major subgroup (the "*Bullia* subgroup") contains the simpler, less sculptured, more inflated forms lacking a reflexed siphonal channel. Before the late Paleocene, this group split to yield the ancestors of the *Calophos* lineage and the ancestors of *Desorinassa* Nuttall and Cooper, 1973.

If the two specimens from the Eocene of Panama (Pl. 11, figs. 4, 5) are accepted as the oldest representatives of *Calophos* Woodring, 1964, this would support a New World origin for this group. The form and location of a pre-Eocene ancestor are unknown. It is conceivable that a Paleogene member of the *Colwellia*/"*Molopophorus*" lineage was involved, but this would necessitate the loss of the recurved siphonal channel in the *Calophos* lineage, or its independent invention in the *Colwellia* group. *Calophos* is the only taxon in the *Bullia* group to evolve representatives in the Caribbean, with apparently endemic species in Trinidad [*C. rohri* (Rutsch, 1942)] and the Dominican Republic [*C. golfoyaquensis* (Maury, 1917)]. The similarity of *Nassa veneris* Faujas de Saint-Fond, 1817 to some of these species suggests that at least one transatlantic crossing may have occurred in this group. The protoconchs of *Calophos* species from Panama and Florida suggest nonplanktotrophic development, and so limited dispersal ability over open ocean. The smaller, more multispiral protoconch of *N. veneris* may indicate no close relationship with New World forms or the origin of planktonic development in one member of the group, which allowed it to disperse to western Europe.

Protoconchs of *Desorinassa* are not sufficiently well-preserved to reveal its mode of development. If it had planktonic larvae, dispersal of its ancestor across the Early Tertiary Atlantic would have presented little problem. If it had nonplanktonic development, then migration could only have occurred along the shallow shelf that joined eastern North America to northwestern Europe in the early Paleogene. A similar pattern of migration has been documented in the large buccinid *Neptunea* Röding, 1798 (Golikov, 1963; discussed by Scheltema, 1979), which has nonplanktotrophic development and seems to have "literally crawled around the arctic continental shelf [a distance of approximately 8500 km] since the Miocene" (Scheltema, 1979, p. 391). A Late Cretaceous–early Paleocene nassariid descendant of *Buccinopsis* could easily have achieved a comparable distance of ~6000 km in a comparable length of time (five to 10 million years).

Two alternatives are available for the ancestry of the New World species assigned to *Bulliopsis* Conrad, 1862a and *Buccinanops* d'Orbigny, 1841. They may be direct descendants of *Desorinassa*, *via* a second transatlantic crossing in the early Eocene (this is about as late as such a crossing could have been achieved by a nonplanktonic form). As discussed in the *Appendix* (p. 119), introduction of molluscan species from Europe to the Gulf Coast reached significant levels in the late Eocene–early Oligocene. It is possible that a *Desorinassa–Bulliopsis* introduction represented the initial stage of this process in the early Eocene. Alternatively, the Gulf Coast Eocene species of *Bulliopsis* could be direct, more or less *in situ* descendants of *Buccinopsis* or a related form and European *Desorinassa* could be descended from *Bulliopsis*. This hypothesis is simpler in requiring only a single west-to-east dispersal event.

Buccinanops is clearly a close relative of *Bulliopsis*. Its exact time and place of origin, however, are less clear. Its oldest representative may be *B.* ? *clarki* Wagner and Schilling, 1923 from the middle to upper Oligocene of California. At the latest, *Buccinanops* dates from the age of the Fuegian/Antarctic species discussed on pp. 79–81, which are probably of early Miocene age. *Buccinanops* apparently arose from part of the *Bulliopsis* lineage in North America sometime between the late Eocene and early Miocene, but it is not possible to be more specific than this at present. An ancestral taxon located in the southeastern U. S. is compatible with early appearances in both western North America and southern South America. As summarized in the *Appendix* (p. 119), there are indications of significant faunal interchange among all three of these regions in the Middle Tertiary. *Buccinanops* could have been one of these westward- and/or southward-moving taxa. Some aspects of this scenario may change as the undescribed species from upper Eocene–lower Oligocene sediments on Seymour Island, Antarctica are exam-

ined in greater detail. The *Buccinanops* lineage could have, for example, experienced an initial diversification in this region before southernmost South America and Antarctica separated in the Middle Tertiary.

The antiquity and geography of the *Buccinanops* lineage mean that the shouldered late Miocene form of *Bulliopsis* from Virginia (herein designated as a new subspecies *B. quadrata bowlerensis*) cannot be directly ancestral to the similarly shouldered *Buccinanops cochlidium* (Dillwyn, 1817), and that this morphology is convergent in the two lineages.

In speculating on the origins of South American species of *Buccinanops*, Ihering (1907, p. 510) suggested that they could only be derived directly from South African *Bullia* s. s., which had in turn been derived from European ancestors. The analysis presented here suggests that this scenario is the least likely one for the evolution of these gastropods, and that the real question is not the origin of South American forms from an essentially Old World group, but rather the origin of South African forms from an essentially New World group. There seem to be at least four possible alternatives for the ancestry of South African (and Indian Subcontinent) *Bullia* Gray, 1834:

(1) They could be independently evolved from a pre-*Buccinanops* nassariid ancestor. This seems unlikely chiefly because it would necessitate extraordinary convergence with South American *Buccinanops*, more than seems reasonable without more substantial evidence than available at present, such as a pre-Pliocene fossil record in Africa.

(2) The ancestors of South African (and Indian subcontinent) *Bullia* could have dispersed from an American Cretaceous ancestor over the chain of islands that may have joined South America and Africa until as late as the early Paleocene [see *Appendix* (p. 117)]. A very ancient *Buccinanops* lineage in South America would be evidence potentially consistent with this alternative and might dispel some objections concerning the extent of required convergence. In the absence of a Paleogene fossil record for the group in Africa, however, it cannot be evaluated further.

(3) The ancestors of South African/Indian *Bullia* could have evolved independently from *Desorinassa* or a similar northwestern European genus in the Early Tertiary, and migrated south in the Neogene. Similarities with South American *Buccinanops* would in this scheme be viewed as parallelisms, derived separately from a common ancestor. The main points arguing against this alternative are the evident lack of significant southward migration of mollusk species in the eastern Atlantic throughout the Tertiary, and the absence of morphologically intermediate living (or fossil) forms between South Africa and Europe.

(4) South African and Indian *Bullia* could be derived from individuals which dispersed from South America via infrequent, chance events such as rafting or dispersal by storms in the late Miocene.

The fourth hypothesis seems the most probable. The absence of a pre-Mio–Pliocene fossil record for the group in Africa and India/Pakistan, discussed above, is not wholly negative evidence. A number of diverse Paleogene molluscan faunas are known from southern and central Africa (see Table 14), and none contain representatives of the *Bullia* group. Dispersal *via* the alternative mechanisms or at earlier dates seem unlikely for the variety of reasons noted.

Direct evidence exists for long-distance dispersal of benthic marine invertebrates lacking planktonic larval stages, but it is largely anecdotal and circumstantial [see Scheltema (1977) and Highsmith (1985), and references therein]. Vagvolgyi (1976) has suggested that the land snail faunas of most Pacific islands are the result of over-ocean dispersal of minute individuals either by winds or on the feet of migrating birds. The latter mechanism might conceivably act for juveniles of larger marine species as well. Other modes of dispersal include passive floating of non-swimming, nonfeeding juveniles, and rafting of adults, juveniles, or eggs on floating vegetation. Rafting on vegetation has been used as an explanation for distributions of reef corals (Jokiel, 1984), bryozoans (Cheetham, 1960), echinoderms (Fell, 1967), ostracodes (Teeter, 1973), and isopods and amphipods (Tully and O'Céidigh, 1986). Edmunds (1977) suggests that at least some patterns of Atlantic opisthobranch distribution can be accounted for by relatively rare, transoceanic dispersal of nonplanktonic (or very short-duration planktonic) species on floating debris or vegetation [see Dell, 1972; Arnaud, 1974; Arnaud *et al.*, 1976; R. D. Simpson, 1977; Pearse, 1979 for further examples].

Kensley (1985a) has reported the isolated occurrence of the Recent South American thaidid gastropod *Concholepas concholepas* (Bruguière, 1789) in Pleistocene terrace deposits on the west coast of southern Africa. He suggests that the fossils "represent a chance pioneer population, established in the Pleistocene (by long distance eastward dispersal of pelagic larvae), long after the South Atlantic had opened up" (Kensley, 1985a, p. 5). Kensley also cites the similar South American–southern African distributions of three living mytilid bivalve species, two of which have been found in the South African Pleistocene, and a living species of brachiopod. While the involvement of pelagic larvae in these cases distinguishes them from that of *Bullia*, they do suggest that Pleistocene transoceanic current conditions could have been appropriate for dispersal of floating debris bearing nonpelagic organisms from west

to east. Exactly this mechanism was proposed by Fell (1962, 1967) to explain the distribution of echinoderms in the Southern Hemisphere. Fell suggested that transoceanic dispersal in this group has consistently been biased in an easterly direction and that South America has acted as a source for several South African species.

Specific examples of trans-oceanic dispersal in marine prosobranchs are rare. Birkeland (1971) suggests that the Pacific buccinid *Searlesia dira* (Reeve, 1856) colonized Cobb Seamount 450 km off the northwest coast of the U. S. by rafting on driftwood. Marche-Marchad (1968) suggests that the wide geographic distribution of the large volutids *Cymba* Sowerby, 1826 and *Adelomelon* Dall, 1906, both of which lack planktonic dispersal stages, might be explained by passive dispersal of their egg capsules. The strongest evidence for the possibility of long-distance dispersal by nonplanktonic representatives of the *Bullia* group comes from Wells and Kilburn (1986), who report the discovery of a single beachworn specimen of *Bullia annulata* (Lamarck, 1816a) on a beach in Western Australia. The eastward-flowing currents that probably carried this shell on a floating log or vegetation from South Africa could also have carried the ancestors of all South African *Bullia* eastward from southern South America.

A number of authors (*e.g.*, Ball, 1976; Nelson and Platnick, 1981; Simberloff, 1983) have objected to "dispersalist" hypotheses as explanations for biogeographic distributions, claiming that they are speculative, *ad hoc*, unfalsifiable, and untestable. These workers complain, with some justification, that long-distance dispersal can and has been used to explain any pattern of distribution without any possibility of refutation or constraint by empirical data. Croizat, Nelson, and Rosen (1974; see also Nelson and Platnick, 1981) go even further and suggest that dispersal across geographic barriers rarely, if ever, occurs, and that allopatric differentiation takes place only as a result of extrinsic barriers arising and separating previously continuous populations.

That such an extreme vicariant view of geographic distribution is unjustified has been demonstrated by, among others, Briggs (1984), who has compiled abundant examples of evolution occurring by the dispersal of new taxa from "centers of origin"[36]. Organisms do in fact disperse over long distances and geographic barriers, and these events may, at least occasionally, be important in their evolution. To discount, *a priori*, all suggestions of long-distance dispersal, furthermore, is to overlook "that the role of [such theories] may be positive and primary, not merely negative and secondary" (Simpson, 1940, p. 156). If all other hypotheses seem much less likely to account for a biogeographic pattern, a dispersal hypothesis may not be only the default, but may be the hypothesis best supported by the data available. It is notable, for example, that the hypothesized dispersal events across the South Atlantic could have occurred as little as 10 or 15 million years after *Buccinanops* seems to have appeared in South America, and so may have occurred almost as soon as could be expected. The hypothesis proposed here can be readily disproven by the discovery of pre-Miocene *Bullia* group fossils in Africa. Dispersal hypotheses may not be strictly falsifiable, but at least some may be testable.

The oldest representative of Nassariinae appears to be from the late Oligocene of Europe (Nuttall, written commun., 1986). Representatives of both Nassariinae and Cylleninae become common in the early Miocene (Cernohorsky, 1984). On the basis of both these ages and their overall morphology, it is possible that these two subfamilies may have arisen from one of the "*Cyllenina*" lineages in the late Oligocene–early Miocene. Testing of this suggestion must await a thorough revision of the European "*Cyllenina*" species as well as of fossil species of *Nassarius* Duméril, 1806 and its close allies.

Some comment should be made here about some of the fossil taxa excluded from the *Bullia* group (see Table 3b). Forms referred to here as the "*Bullia*" *altilis* complex [*i.e.*, "*Bullia*" *altilis* (Conrad, 1832b), "*B.*" *altilis subglobosa* (Conrad, 1832b), "*B.*" *calluspira* (Dockery, 1980), "*B.*" *tuomeyi* (Aldrich, 1921), "*Ancillopsis*" *patula* (Deshayes, 1835), "*Buccinanops*" *ellipticum* (Whitfield, 1865)], from the Eocene of the southeastern U. S. and Paris Basin, bear some general resemblance to some living species of *Bullia* s. s. from South Africa (cf. figs. on Pls. 2 and 9), particularly in overall shell form and form of the terminal portion of the columella. I consider these resemblances to be convergent, rather than indicative of an ancestor–descendant relationship (as assumed, for example, by Cossmann, 1901b, and Ihering, 1907), chiefly because there is no evidence for evolutionary intermediates in the appropriate stratigraphic and biogeographic positions. These Gulf Coast and European forms represent a very distinct suite of morphologies characterized by extreme simplification of form and sculpture, often accompanied by pronounced parietal callus development, body whorl enlargement, and spire reduction. There is no positive morphological evidence linking them to the *Bullia* group, and they should not be included in this group unless such evidence can be specified. They should be viewed as having independently

[36] These centers need not be the geographic locations of the origins of the entire group, but only of abundant new lineages within the group.

achieved a shell form somewhat similar to that of some living species of *Bullia* s. s., but 40 million years earlier and on the other side of the equator. These forms will require a detailed study of their own for their systematic position to be determined.

Several authors (*e.g.*, King, 1953; Tankard, 1975; Tankard and Rogers, 1978) have noted that Late Tertiary through earliest Quaternary macrofossil assemblages from South Africa indicate warmer conditions during that time than those prevailing today. The invertebrate faunas furthermore are more or less cosmopolitan across all of southern Africa, with provinciality and distinction between Indian and Atlantic Ocean faunas much reduced relative to their present levels (Tankard and Rogers, 1978). As a result of lower provinciality, the total diversity of the Neogene marine fauna of South Africa appears to have been significantly lower than at present. Since the middle Miocene, there has been an increase in provinciality and total diversity in the region. This correlates with an overall cooling, or equatorward shift in provincial boundaries, associated with the onset of continental glaciation on Antarctica (Tankard, 1975; Kennett, 1977, 1978). This event reduced the dominance of tropical forms and increased that of subtropical and temperate taxa (Tankard and Rogers, 1978). It is interesting to note that this major change in patterns of marine communities around southern Africa appears to occur at around the time of the first known representatives of the *Bullia* group in the area.

While the species of Nassariinae and Cylleninae have their centers of diversity in tropical latitudes and appear to have always preferred warmer waters (Cernohorsky, 1984), species of the *Bullia* group are, and seem to have been throughout their history, more partial to subtropical to temperate conditions. They are absent from the Tethyan–Caribbean area (with the exception of two species of *Calophos*), and from the diverse warm-water faunas of the Eocene Paris Basin. This may explain the apparent non-response of the group to the major climatic events of the Cenozoic that appear to have affected many warmer-water molluscan taxa (see, *e.g.*, Stanley, 1984, 1986).

Systematic Summary

On the basis of the fossil and Recent data summarized here, I suggest that the living species of the *Bullia* group be placed into two genera, *Dorsanum* Gray, 1847 and *Bullia* Gray, 1834, the later being divided into two subgenera. Brief justification for this decision follows.

The range of conchological variability is actually much greater among the Recent species assigned to *Bullia* s. s. than between these species and *Dorsanum miran* (Bruguière, 1789) (cf. *e.g.*, Pls. 1, 2). *Bullia rhodostoma* Reeve, 1847, for example, is in many ways more similar to *Dorsanum miran* than to *B. vittata* (Linnaeus, 1767). Nevertheless, *D. miran* appears to show consistent conchological differences distinguishing it from the other species: (1) two pronounced oblique spiral carinae bounding a reflexed siphonal channel around the anterior end of the fasciole [species of *Bullia* s. s. and *Buccinanops* lack this channel and have only one carina posterior to the fasciole]; (2) a pronounced terminal columellar fold [this character is present in *Buccinanops* but variable in *Bullia* s. s.]; (3) differences in protoconch form, as discussed on pp. 17, 18; (4) differences in sculpture of the early teleoconch, as discussed on p. 19.

Dorsanum miran (Bruguière, 1789) is also distinct in a number of non-shell characters: (1) lack of posterior metapodial tentacles; (2) short antennae; (3) planktonic larval stage; (4) bicuspid lateral radular teeth; and (5) eyes. Recognizing that the shell of *Dorsanum* differed little from those of other related taxa, Cossmann (1901b, p. 219) also noted that the distinctiveness of the genus lay chiefly in features of soft part anatomy.

In summary, *Dorsanum miran* (Bruguière, 1789) consistently shows a suite of characters that distinguish it from all other Recent species. Furthermore, although little is known about the ecology of *Dorsanum*, what is known of the ecology of living *Bullia* s. s. suggests that the latter is quite distinct, perhaps even warranting the appelation of inhabiting a distinct "adaptive zone" (see, *e.g.*, Simpson, 1961; Mayr, 1969). This taxonomic conclusion, based solely on information from living species, is reinforced by consideration of fossil taxa, as discussed on p. 105.

The apparent relationship of Recent species of *Bullia* s. s. to *Buccinanops* d'Orbigny, 1841 reinforces this interpretation of *Dorsanum*. I place the South American species of *Buccinanops* as a subgenus under the genus *Bullia* for the following reasons: (1) the ranges of conchological variation of these two groups of species overlap considerably (cf. figs. on Pls. 2 and 3). If they were co-occurring it would be difficult to demonstrate any morphological gap between them, the chief difference being the consistent presence of a terminal columellar fold and occasionally much larger size in *Buccinanops*. (2) They have in common nonplanktonic larval development and blindness. (3) Analysis of fossil representatives of the *Bullia* group suggests that *Bullia* of South Africa is the direct descendant of *Buccinanops* from South America.

Throughout this paper, nassariid species not belonging to the subfamilies Nassariinae or Cylleninae, such as the "*Bullia* group", have been treated as a single evolutionary entity, essentially equivalent to Cernohorsky's (1984) use of the subfamily Dorsaninae. If the

evolutionary history portrayed in Text-figure 1 is largely correct, however, at least two monophyletic taxa are recognizable within the "*Bullia* group". One containing the *Colwellia*/"*Molopophorus*" group from the West Coast of North America, the European fossil forms *Pseudocominella* Nuttall and Cooper, 1973, *Keepingia* Nuttall and Cooper, 1973, *Whitecliffia* Nuttall and Cooper, 1973, at least some species of "*Cyllenina*", and the living species *Dorsanum miran* (Bruguière, 1789), can be referred to as the subfamily Dorsaninae. The other (the "*Bullia* subgroup") includes the genus *Calophos* Woodring, 1964, as well as *Desorinassa* Nuttall and Cooper, 1973 and its close relatives *Bulliopsis* Conrad, 1862a, *Buccinanops*, and *Bullia*. The subfamilial name Bulliinae is proposed for this group.

The genus *Thanetinassa* Nuttall and Cooper, 1973 and other species of "*Cyllenina*" appear to be more closely related to Nassariinae than to the *Bullia* group, and may be referable to this taxon. Should future work indicate that other, non-nassariid taxa evolved from something like *Thanetinassa*, then Nassariinae would be paraphyletic. This supraspecific classification is surely not what would have (and has in the past) resulted from consideration of only living taxa. *Bullia* s. s. and *Dorsanum miran* (Bruguière, 1789) do not really look different enough, in and of themselves, to justify their placement in separate subfamilies. It is their evident positions on different branches of the nassariid family tree (a tree composed largely of extinct taxa preserved in the fossil record) that supports their taxonomic separation.

The classification of the Nassariidae derived from this study is shown in Table 16.

Table 16.—Classification of the Nassariidae derived from this study. Genera of Nassariinae and Cylleninae are taken without modification from Cernohorsky (1984); subgenera are not listed. Poorly defined genus-level groups in need of revision are enclosed in brackets [ ].

Class Gastropoda Cuvier, 1797
  Subclass Prosobranchia Milne-Edwards, 1848
    Order Neogastropoda Thiele, 1929
      Superfamily Muricoidea Rafinesque, 1815[1]
        Family Nassariidae Iredale, 1916
          Subfamily Nassariinae Iredale, 1916
            Genus *Nassarius* Duméril, 1806
            Genus *Hebra* Adams and Adams, 1853
            Genus *Demoulia* Gray, 1838
            Genus *Cyclope* Risso, 1826
          Subfamily Cylleninae Bellardi, 1882
            Genus *Cyllene* Gray, 1834
          Subfamily Dorsaninae Cossmann, 1901b
            Genus *Dorsanum* Gray, 1847
            *Genus *Keepingia* Nuttall and Cooper, 1973
            *Genus *Pseudocominella* Nuttall and Cooper, 1973
            *Genus *Whitecliffia* Nuttall and Cooper, 1973
            *Genus *Colwellia* Nuttall and Cooper, 1973
            *[Genus "*Molopophorus*" Gabb, 1869]
            *[Genus "*Cyllenina*" Bellardi, 1882]
          Subfamily Bulliinae Allmon, new subfamily[2]
            Genus *Bullia* Gray, 1834
            Subgenus *Bullia* Gray, 1834
            Subgenus *Buccinanops* d'Orbigny, 1841
            *Subgenus *Bulliopsis* Conrad, 1862a
            ? Subgenus *Cereobullia* Melvill and Peile, 1924
            *Genus *Calophos* Woodring, 1964
            *Genus *Desorinassa* Nuttall and Cooper, 1973
          Subfamily Uncertain
            Genus *Thanetinasa* Nuttall and Cooper, 1973
            [Genus "*Adinopsis*" Odhner, 1923]
            [Genus Uncertain]
              [*Bullia* ? *granulosa*]
              [*Bullia* ? *terebraeformis*]

* Taxa known only from fossils.
[1] Name translated by Thiele, 1929.
[2] *Type genus.*—*Bullia* Gray, 1834.

Diagnosis.—Shells differ from those of Dorsaninae in lacking a well-developed recurved siphonal channel, bounded by sharp carinae, extending from the anterior notch around the dorsal side to the fasciole. External and internal sculpture usually reduced compared to most members of Dorsaninae. Only *Calophos* shows pronounced striae or ridges inside the outer apertural lip. Some species of *Calophos* and *Bullia* (*Buccinanops*) show development of axial sculpture on the teleoconch; otherwise shells are smooth. Relative spire height variable. Pronounced terminal columellar fold usually present, except in most living species of *Bullia* (*Bullia*). Average size of shell approximately the same as in Dorsaninae, although representatives of *Bullia* (*Buccinanops*) can occasionally exceed 50 mm total height. Development probably nonplanktotrophic in most genera. Recent species lack eyes, have one or two posterior metapodial tentacles, multicuspidate lateral radular teeth, relatively very large foot, and are intertidal to shallow subtidal in habit.

APPENDIX

Paleobiogeographic History of the Atlantic

North Atlantic Plate Movements

Oceanic crust appears to have first formed between Africa and North America between 165 and 140 ma, with Africa sliding eastward relative to Europe along a major fracture zone (Pitman and Talwani, 1972; Sclater, Hellinger, and Tapscott, 1977; Hallam, 1981). A shallow epicontinental seaway linking Central America with southern Europe and North Africa may have been established, at least intermittently, by the late Early or early Middle Jurassic, but actual rifting between North America and Africa does not seem to have created fully marine conditions in this area until Callovian–Oxfordian times (165–140 ma). By about 125 ma, Eurasia and Africa severed their last point of connection at the Iberian Peninsula. By at least the Early to Middle Cretaceous (110 ma), if not before, North and South America were separated, allowing a connection between the Atlantic and Pacific, and thus the establishment of the circumequatorial Tethys seaway (Berggren and Hollister, 1974; Sclater, Hellinger, and Tapscott, 1977). The next part of the North Atlantic to open was between Newfoundland and Ireland beginning in the Middle Cretaceous [90–95 ma] (Hallam, 1981). Although there seems to have been shallow water between Greenland and Canada in the Campanian, preventing terrestrial biotic connection during that time (McKenna, 1983), rifting between these areas probably did not begin until around 73 ma [Late Cretaceous] (Berggren and Schnitker, 1983). This spreading stopped by the late Eocene–early Oligocene (approximately 36 ma), after which time Greenland was tectonically a part of North America.

Although Sclater, Hellinger, and Tapscott (1977) have suggested that Greenland began to separate from Europe as early as 90 ma, most other authors maintain that the Norwegian Sea did not begin to open until 50–65 ma (Berggren and Hollister, 1974; Eldholm and Thiede, 1980; Hallam, 1981; Berggren and Schnitker, 1983; Williams, 1986), and that the existence of pre-Cenozoic oceanic crust is unlikely (Talwani and Eldholm, 1977; Eldholm and Thiede, 1980).

The history of the Norwegian–Greenland Sea is complex, much of this complexity being due to a major feature known as the Greenland–Scotland Ridge (GSR), an elongate structural high on the ocean floor, stretching between Greenland and northern Scotland. The GSR is composed of several sections, including the Greenland–Iceland ridge, the Iceland–Faeroe Ridge, and the Wyville–Thomson Ridge (between the Faeroe Islands and Scotland), as well as the insular platforms of Iceland and the Faeroes themselves. The Jan Mayen Ridge off eastern Greenland may also be part of this complex (see Williams, 1986).

The GSR consists of elevated ocean crust, subaerial and submarine volcanic plateaus, continental microfragments, and sedimentary deposits (Nilsen, 1983). It seems to have originated as a subaerial volcanic ridge, which grew continuously as Greenland separated from Europe (Nunns, 1983; Thiede and Eldholm, 1983). Much of its complexity may be due to episodes or cycles of rifting, volcanism, and subaerial and submarine erosion (Nilsen, 1983). A terrestrial connection (often known as the Thulean land bridge) existed between North America and Europe *via* the GSR until the early Eocene (McKenna, 1983), when the ridge began to subside. The main portions of the ridge seem to have been emergent until the middle Miocene, with isolated peaks remaining above sea level until the Pliocene (Nunns, 1983; Thiede and Eldholm, 1983).

A land connection appears to have persisted between Svalbard and northern Greenland until the late Eocene–early Oligocene (McKenna, 1975, 1983; Hallam, 1981), after which time the last possible terrestrial (and shallow shelf) continuity between the two sides of the North Atlantic was eliminated. Marincovich, Brouwers, and Carter (1985) have suggested that during times of high sea level in the Paleocene, a shallow seaway intermittently connected the Arctic Ocean with the North Sea basin, *via* the Norwegian–Greenland Sea. There may also have been limited, shallow-water connection between the North Sea and the Atlantic at this time. A deep-water connection between the Arctic and Atlantic Oceans was finally established between 45 and 35 ma (late Eocene). Cold deep water from the Arctic began to flow into the North Atlantic, and this coincided with a sharp decline in bottom temperatures worldwide (Berggren and Hollister, 1974; Berggren and Schnitker, 1983).

The Tethyan ocean closed as it had opened in a series of events. Africa–Arabia appears to have collided with Eurasia in the vicinity of what is now the Middle East in the late Oligocene–early Miocene (Benson, 1979; Rögl and Steininger, 1984). Land mammal faunas began to be exchanged between the two continents in the early to middle Miocene (Savage, 1967; Berggren and Phillips, 1971; Rögl and Steininger, 1984, and references therein). Northwestern Africa made contact with the Iberian peninnsula in the middle to late Miocene, temporarily closing off contact between the Mediterranean and the Atlantic between five and six million years ago (Van Couvering *et al.*, 1976; Adams *et al.*, 1977; Benson, 1979).

South Atlantic Plate Movements

The Lower Jurassic (~180 ma) Ferrar Supergroup of West Antarctica is a set of intrusive and extrusive igneous rocks that marks the beginning of the breakup of Gondwanaland (Elliott, 1985). Within 20 million years, the first ocean floor basalt was generated in what is now the Weddell Sea (LaBreque and Barker, 1981). Antarctica separated from southern Africa by the Early Cretaceous (approximately 145 ma), and by the late Early Cretaceous (120 ma), significant spreading had occurred between the two continents (Dingle, Siesser, and Newton, 1983; Elliott, 1985). This spreading continued into the Tertiary until the present separation of approximately 4000 km between the Cape of Good Hope and Antarctica was reached in the Late Tertiary. Although the Early Cenozoic geological history of the area is difficult to evaluate, continuous land connection between Antarctica and southern South America probably ceased to exist by the Paleocene (Williams, 1986). Shallow marine shelf connected the two continents until the late Oligocene–early Miocene (25–30 ma) when the Drake Passage opened, establishing deep-water conditions, and probably allowing development of the circum-Antarctic current (Kennett, 1977; Woodburne and Zinsmeister, 1984; Elliott, 1985).

The oldest magnetic anomalies in the South Atlantic are found in the Cape Basin off the western coast of South Africa, dated at approximately 120–130 ma (Larson and Ladd, 1973; E. S. W. Simpson, 1977; Sclater, Hellinger, and Tapscott, 1977; Hallam, 1981), and this seems to be a generally agreed-upon date for the initial opening of the South Atlantic. While the first marine incursion between Africa and South America seems to have taken place at about this time (Reyment, 1980), farther north the first results of rifting may have been the formation of large freshwater lakes, similar to the modern African Great Lakes or Lake Baikal (Sclater, Hellinger, and Tapscott, 1977). Reyment and Tait (1972) discuss major deposits of lacustrine sediments found on the opposing shores of the two continents.

The tectonic history of the South Atlantic is divisible into two major stages. In the first, rifting occurred between West Africa and southern South America; what are now westernmost Africa and easternmost South America remained together. A major reorientation of spreading regime occurred at about 80 ma, following which North Africa and eastern South America began to move apart, and the two continents subsequently diverged more or less in parallel (Berggren and Hollister, 1974; E. S. W. Simpson, 1977).

The first passage of marine organisms between the North and South Atlantic appears to have occurred in the late Albian (100–105 ma) *via* a shallow marine connection (Sclater, Hellinger, and Tapscott, 1977; Reyment, 1980). Reyment (1980) and Melguen, Le Pichon, and Sibuet (1978) believe that the establishment of deep oceanic conditions between the North and South Atlantic was achieved between 80–90 ma. Sclater, Hellinger, and Tapscott (1977), however, suggest that deep water might have been established as late as earliest Tertiary (60 ma).

As in the North Atlantic, the history of the South Atlantic is complicated by the presence of a large aseismic ridge complex made up of the Walvis Ridge, which stretches from the western coast of southwest Africa westward to near the Mid-Atlantic Ridge, and the Río Grande Rise, which runs from near the northern coast of Patagonia eastward to near the Mid-Atlantic Ridge (Text-fig. 26). Both of these structures appear to have been of volcanic origin due to some form of "hotspot" activity (Thiede, 1977; Gamboa and Rabinowitz, 1981). Based on DSDP data from both areas, it has been suggested that these ridges originated in the Late Cretaceous (Santonian–Campanian, 75–85 ma) as subaerial volcanic ridges, standing perhaps as high as 2000 m above sea level (Thiede, 1977; E. S. W. Simpson, 1977; Gamboa and Rabinowitz, 1984). Much or most of this system may have become submerged by Late Cretaceous (Hallam, 1981). Melguen, Le Pichon, and Sibuet (1978) and Reyment (1980; see additional references therein) have suggested, however, that areas of these ridges were exposed as a chain of sizeable islands across the South Atlantic at least into the Paleocene. After this time the ridges ceased to form an effective barrier between the basins of the North and southernmost South Atlantic (Thiede, 1977; Sclater, Hellinger, and Tapscott, 1977; Reyment, 1980), although to this day the Walvis Ridge acts as an effective barrier to cold water, organisms, and nutrients entering the Angola Basin (E. S. W. Simpson, 1977, p. 13). Such a chain of large islands, suggests Reyment (1980, p. 131), could have provided an arrangement "enabling many organ-

isms to cross the South Atlantic at an advanced stage of opening." Benson (1988) has recently disputed this reconstruction.

The Late Mesozoic and Cenozoic history of the circum-Atlantic area is summarized pictorially here in four paleogeographic maps (Text-figs. 26–29). These maps are intended to show in a generalized way the patterns of change in the distribution of land and shallow and deep seas, especially as they would have affected benthic marine invertebrates such as species of the *Bullia* group. Superimposed on these maps are a series of arrows, representing the hypothesized routes of dispersal of various members of the group, as discussed on pp. 110–113.

Paleobiogeographic Patterns

Despite their abundance, diversity, generally good preservation, and substantial amount of taxonomic attention they have received, Paleogene molluscan faunas from the circum-Atlantic region have yet to be thoroughly studied biogeographically. Until such synthetic studies are done, one can cite only limited work on particular areas or taxonomic groups. The major difficulty with attempting to use previously published molluscan faunas for biogeographic comparison, especially across the Atlantic, is that one is never sure that the same taxa are being referred to by the same name. The taxonomic confusion within the *Bullia* group is just one small example of this problem. Conclusions on Tertiary molluscan biogeography must therefore be approached with caution.

Sohl (1964) has reviewed the relationships of Upper Cretaceous gastropod faunas in the New and Old Worlds, and shows that the Senonian faunas of Pondoland, South Africa are the most similar to those of the southeastern U. S. of any outside North America. The South African Cretaceous fauna, says Sohl, "appears to have been a melting pot with free access to both the Gulf Coast [of the U. S.] and to India". According to Sohl's summary, while the Cretaceous faunas of the Gulf Coast and West Africa share a large number of taxa, those of Brazil and the southeastern U. S. share relatively few.

Turner (1973) has attributed similarities in Late Cretaceous eastern North American (New Jersey) and European bryozoan faunas to a still unbroken continental shelf between these two areas, which allowed stepwise larval dispersal in a group that today is strongly dominanted by species having low-dispersal nonplanktotrophic larvae. As summarized above, in the Early Tertiary, North America (including Greenland) and Europe were still essentially continuous, allowing not only land mammals to be freely exchanged, but also benthic marine invertebrates that were limited to shallow shelves (Berggren and Hollister, 1974, p. 150). Molluscan faunas from the Danian of West Greenland indicate warm temperate conditions in that area at that time, a suggestion supported by paleobotanical evidence (Rosenkrantz, 1970; Kollmann and Peel, 1983). The molluscan fauna contains several bivalve species comparable to species from the upper Paleocene Aquia Formation of Maryland and the Thanetian of the Paris Basin (Rosenkrantz, 1970, p. 447). According to Kollmann and Peel, West Greenland Paleocene turritellid gastropods show closest affinities with European taxa. The widespread gastropod genus *Pseudoliva* Swainson, 1840, which is present in the Gulf Coast, is also represented. Cooler conditions seem to have developed in the North Atlantic by the Eocene (Berggren and Hollister, 1974). Lower to middle Eocene molluscan faunas from East Greenland (Ravn, 1904) contain typical cold-water taxa and lack characteristic warm-water forms.

On the eastern side of the Atlantic, Africa seems to have been faunally distinct from Europe throughout much of the Cenozoic. Although Newton (1922) believed that one-third of the 72 species of mollusks he described from the Eocene of southern Nigeria showed close affinities with Anglo–French–Belgian faunas, Eames (1957), on revising Newton's work, claimed that no northwest European forms were present. Adegoke (1977) similarly concludes that West African Paleogene faunas show little or no affinity to contemporaneous European faunas. These African faunas, however, do share elements with those of the U. S. Gulf Coast, the Soldado Formation of Trinidad, and the Maria Farinha Formation of Brazil (Adegoke, 1977, p. 43). During the Paleogene, the Mediterranean region and eastern Tethys (now the Indian Ocean) formed a uniform biogeographic province (Adams, 1967; Berggren and Hollister, 1974; Vermeij, 1978, p. 227). Although the Atlantic was well-developed at low latitudes by this time, some Indo-European taxa occurred as far west as the Caribbean region (Berggren and Hollister, 1974). This pattern of faunal resemblance has been noted by many workers, who frequently mark the observation by referring to the occurrence of "Tethyan" taxa in the New World. Biogeographic data are not yet refined enough to confirm or disprove this pattern, but some transatlantic comparisons of two groups, in particular the mollusks and larger foraminifera, seem suggestive.

The Paleocene Maria Farinha Formation, exposed in the state of Pernambuco, Brazil, contains nautiloids and turritellid and buccinid gastropods that seem to show close relationships with taxa from the Midway Group of the U. S. Gulf Coast (Gardner, 1931, 1935; Woodring, 1972). Both Gulf Coast and Brazilian faunas show some affinities with the Caribbean Paleocene as represented by the fauna of the Soldado Formation of Trinidad (Maury, 1912, 1924–1927, 1925, 1929; Waring, 1926; Rutsch, 1942; Woodring, 1972; Kugler and Caudri, 1975). Davies, Eames, and Savage (1975, p. 128) have suggested that the Paleocene Midway faunas of the Gulf Coast show greater similarities with the "boreal" faunas of northwestern Europe than with lower latitude faunas. Gardner (1931, 1935), on the other hand, emphasized the Tethyan affinities of the Midway: "The Midway fauna of Texas is unmistakably a part of the homogeneous biota which lived on the warm and warm temperate shores of the Gulf of Mexico and as far south as Brazil, and is less definitely a part of the more heterogeneous biota originating in the inshore waters of the old Tethyan sea." (Gardner, 1931, p. 160)

Palmer (1957, 1967, 1974; see also Davies, Eames, and Savage, 1975, p. 163) considered two faunal provinces to be recognizable in the New World during the Paleocene and Eocene: (1) a Gulf and Atlantic coastal plain province, characterized by bivalves of the *Venericardia* (*Venericor*) *planicosta* species group, includes the eastern North American coastal plains, northern South America, parts of the west coast of North America, and at least parts of the Anglo–French–Belgian Basin; (2) a "Tethyan" province, characterized by the neritid gastropod *Velates perversus* (Gmelin, 1791), recorded from India, Burma, Bonin Island (western Pacific), the Paris Basin, Hungary, Italy, Germany, Spain, Switzerland, Armenia, Iran, Egypt, Arabia, East Africa, Madagascar, Somalia, Jamaica, Panama, Florida, St. Bartholomew, possibly the Dominican Republic, and California (see Vokes, 1935; Squires, 1986). It seems likely that the taxonomy of these two mollusk groups is in need of revision, and that the occurrences as listed here are not totally accurate. Other, more general comparisons, however, seem to show similar patterns. Richards and Palmer (1953; see also Palmer and Richards, 1954), for example, described a molluscan assemblage from the Eocene of Florida that showed surprisingly few similarities with other Gulf Coast Paleogene faunas, but very strong similarities to contemporary European faunas.

This degree of faunal heterogeneity within the Gulf of Mexico/Caribbean region correlates well with the apparent duration of a marine connection between the Gulf and the Atlantic in the Late Cretaceous and Early Tertiary through the Suwanee Strait or Channel (Hull, 1962; Cheetham, 1963; Chen, 1965; McKinney, 1984; Pinet and Popenoe, 1985), which stretched across southern Georgia and northern Florida. Strong flow through this strait "produced a sharp facies boundary that separated clastic deposits from the Appalachian Piedmont from carbonate deposits produced in situ over the Florida

Platform." (Pinet and Popenoe, 1985, p. 619). Givens (1989) has recently provided a list of 46 primarily Tethyan mollusk genera that occur in lower and middle Eocene deposits on the Gulf Coast. This suggests that the biogeographic barrier separating the mainly warm-water, carbonate-substrate Floridian fauna from the cooler-water, mainly clastic-substrate Gulf Coast fauna during the Eocene was at least semipermeable.

The connection between northwestern Europe and the U. S. Gulf and Atlantic coasts in the early Paleogene is less clear. Marincovich, Brouwers, and Carter (1985) have suggested that north central North America and northwestern Europe were connected to the Arctic Ocean in the Paleocene, forming a semi-isolated boreal molluscan province, separate from the North Atlantic and Gulf of Mexico.

Larger foraminifera show an overall pattern of decreasing similarity between the western Atlantic and Tethys through the Tertiary. An exception to this pattern is the most common Paleogene genus of larger foraminifera, *Nummulites* Lamarck, 1801. Although Hottinger (1973) states that the group is too poorly understood taxonomically to allow reliable biogeographic conclusions, some observations can be made. *Nummulites* arose in the Paleocene, probably in western Tethys (Adams, 1967), and quickly achieved a wide distribution throughout the Tethyan region. This distribution expanded still further into the early Eocene, when it ranges from southeast Asia and the Indo-Pacific to western Europe and West Africa. Not until the late Eocene, however, did *Nummulites* reach the New World (Davies, Eames, and Savage, 1975, p. 203). Two species occur in late Eocene sediments in the West Indies, Florida, Panama, and the boundary region between Peru and Ecuador (Adams, 1967; Davies, Eames, and Savage, 1975). Today, *Nummulites* is restricted to the Indo-Pacific (Brasier, 1980). Other taxa of larger foraminifera appear to have arisen in the Americas and to have spread eastward (Adams, 1967, 1973, 1983; Caudri, 1975). In general, data for larger foraminifera do not support the view that Caribbean Paleogene faunas had a Tethyan character, despite the two regions sharing perhaps four of 12–15 genera (Adams, written commun., 1985). If these common taxa arose in the Americas it would be more accurate to refer to a New World influence on Tethyan faunas. If there was significant biogeographic heterogeneity in the Caribbean area, it is definitely not reflected in the distribution of larger formaminifera after the middle Eocene, when Caribbean, Gulf Coast, and West Coast faunas become essentially similar (Adams, written commun., 1985).

In summary, based on the limited evidence available, the distribution of larger foraminifera suggests some degree of contact between Tethyan and American faunas in the Early Tertiary, although the sources and extent of this affinity remain obscure. Adams (1967, p. 211) concludes that "the Atlantic constituted a major barrier to migration throughout the whole of the Tertiary. It did, however, permit occasional crossings in both directions — probably in exceptional circumstances as when large masses of weed were detached from the sea floor in the Caribbean area during hurricanes."

In the northern Atlantic, strong general similarities seem to exist between Caribbean–Gulf and Atlantic coastal plain Midwayan-age foraminiferan faunas and southern Scandinavian and Polish Paleocene faunas (Berggren and Hollister, 1974).

Middle Eocene molluscan faunas on the two sides of the Atlantic show both similarities and differences. Davies, Eames, and Savage (1975, pp. 177–178) list 18 genera of bivalves and gastropods as occurring in the Lutetian of the Paris Basin but not in the contemporaneous Claiborne beds of the Gulf Coast. According to Abrard (1925; cited by Davies, Eames, and Savage, 1975, p. 178), only three molluscan species are common to the Eocene of the Paris Basin and Alabama.

The introduction of molluscan species from Europe to the Gulf Coast may have reached significant levels at or around the Eocene–Oligocene transition (Dockery, 1984). Although there are few examples of species common to early Oligocene faunas of the two areas, a number of species are very similar.

The relationship of the Paleogene molluscan faunas of the Gulf Coast to those of the Pacific Coast of North America needs to be investigated in greater detail. Based on the data currently available it seems to have been one of "partial communication with barriers of unequal value for different forms of life." (Davies, Eames and Savage, 1975, p. 130) Affinities of West Coast faunas with those of the West Indies seem to be closer. Palmer (1967) noted that "Tethyan" forms occur together with members of the *Venericardia planicosta* group and typical Paris Basin genera in lower and middle Eocene strata of southern California. Davies, Eames and Savage (1975) state that species of several Tertiary mollusk genera from the West Coast of North America are similar to or identical with congeners from the Soldado fauna of Trinidad. Similar conclusions have been reached by Smith (1975) and Keen (1976).

Zinsmeister (written commun., 1985) has suggested that the venerid bivalve genus *Amiantis* Carpenter, 1864 is one of several molluscan taxa that seems to have arisen in North America and subsequently migrated to the coasts of South America. *Amiantis,* or something very like it, is known from the Oligocene or Miocene of California and the Eocene of Colombia, and something like it lives today from California to Mexico (Clark, 1946; Palmer, 1927, p. 304; Cox *et al.*, 1969, p. N675; Abbott, 1974, p. 532). *Amiantis* seems to have arrived on the Patagonian coast sometime during the Miocene, and it is a conspicuous member of faunas in Patagonia and Chile throughout the remainder of the Cenozoic (Zinsmeister, written commun., 1985). Again, the problem with this example in the present context is the lack of sufficient taxonomic comparison to insure that all forms referred to this genus by various authors actually belong to it. Further work is required to evaluate this and other putative instances of southward migration of American molluscan taxa in the Middle Tertiary.

The Anglo–French–Belgian Basin shares relatively few taxa with the "Tethyan" province throughout the Paleogene. The sea that occupied this basin during the Thanetian was apparently more open to the north than to the west, and its connection to the developing Atlantic was probably a narrow one through the present English Channel (Davies, Eames, and Savage, 1975, p. 104). Some connection probably did exist between this northern basin and Tethys, however, between Ypressian and Lutetian times, *via* the Atlantic, and some Tethyan taxa entered it during this period.

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EXPLANATION OF PLATE 1

Representative Recent species of *Nassarius* and *Cyllene*, the single Recent species of *Dorsanum*, and other Recent species of uncertain affinities related to the *Bullia* group

Figure — Page

1a, 1b. *Nassarius arcularia* (Linnaeus, 1758) 11
MCZ(M) 296860, Moluccas, height = 25.0 mm. Type species of the genus *Nassarius* Duméril, 1806.

2. *Nassarius retecosa* Adams, 1852 11
MCZ(M) 296861, Mauritius, height = 18.4 mm.

3. *Cyllene desmoversi lamarcki* Cernohorsky, 1975 11
MCZ(M) 201966, Joal, Senegal, height = 17.0 mm.

4. *Adinus truncatus* (Reeve, 1846) 29
ANSP 34615 (no locality information available), height = 37 mm.

5–7. "*Adinopsis*" *skoogi* Odhner, 1923 29
5, 6. ANSP 334519, trawled from 90 m depth, 4°55′ S, 11°32′ E, coast of Zaire, Gulf of Guinea. 5, height = 33 mm [Note slit at edge of parietal callus, more pronounced terminal columellar fold, and faint apertural striae in this larger specimen]; 6, height = 27 mm.
7. Paratype (unnumbered IRSNB specimen), Porto Alexander, Angola, height = 24.4 mm (from Adam and Knudsen, 1984, pl. 5, fig. 9).

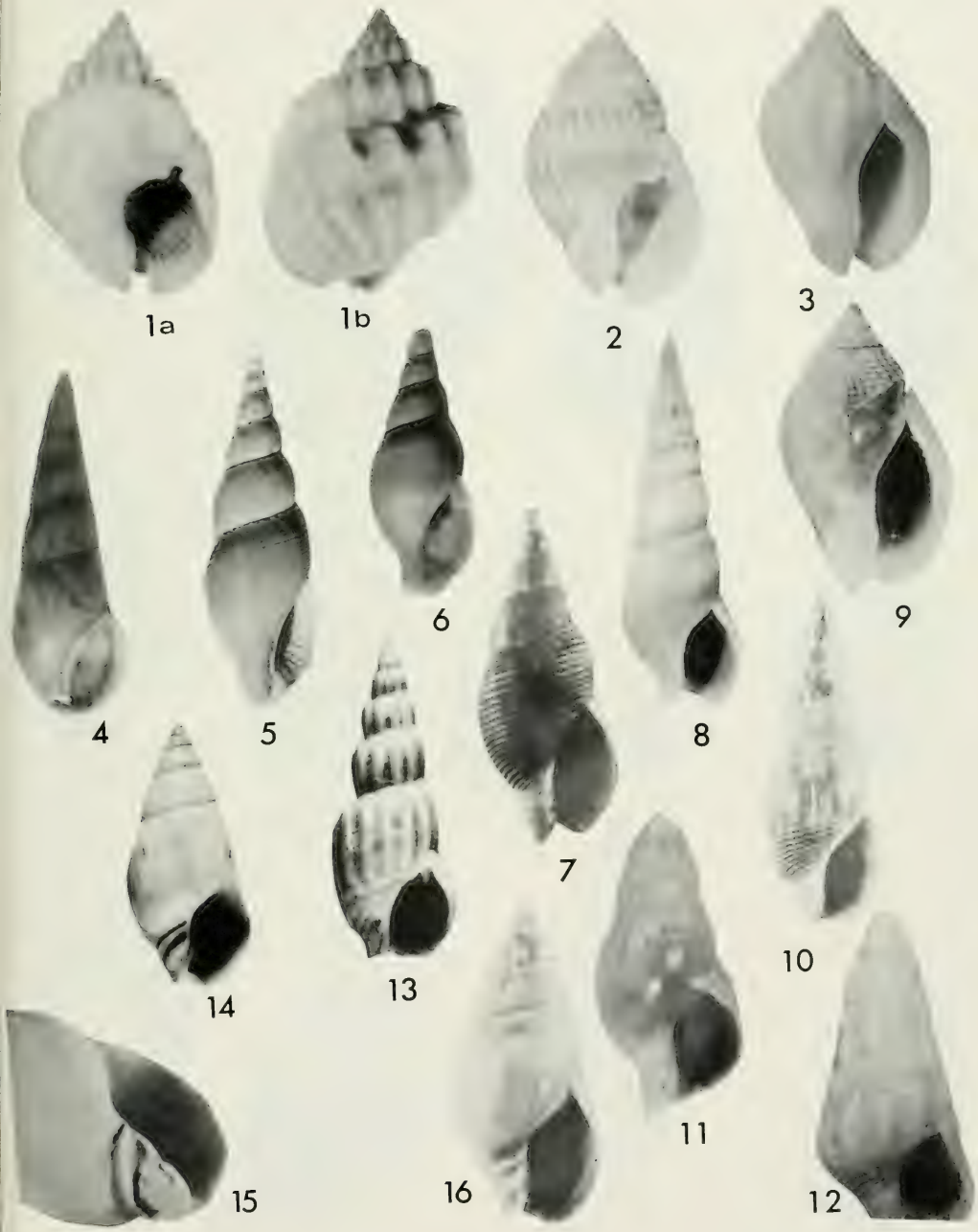
8, 11. "*Bullia*" *granulosa* (Lamarck, 1822) 28
8. MCZ(M) 296220, Persian Gulf or Mekran Coast, height = 31.0 mm.
11. IRSNB–Dautzenberg collection, I.G. 10.591, Zaire River estuary, height = 7.1 mm.

9. *Cyllene owenii* Gray, 1834 11
MCZ(M) 214118, Sierra Leone River, Freetown, Sierra Leone, height = 17.5 mm.

10, 12. "*Bullia*" *terebraeformis* (Dautzenberg, 1913) 28
10. Syntype (unnumbered IRSNB specimen), 15–20 m depth, Mossamedes Bay, Angola, height = 24.0 mm (from Adam and Knudsen, 1984, pl. 5, fig. 10).
12. Syntype (IRSNB–Dautzenberg collection, I.G. 10.591), Mossamedes Bay, Angola, height = 7.6 mm.

13. *Bullia ceroplasta* Melvill, 1898 19
Mekran, Arabian Sea, height = 13.5 mm (from Cernohorsky, 1984, fig. 93).

14–16. *Dorsanum miran* (Bruguière, 1789) 27
14. MCZ(M) 133727, Gambia, height = 29.0 mm.
15. MCZ(M) 296221 (no locality data available), height = 25.7 mm. Closeup of fasciole showing recurved siphonal channel.
16. Dakar, Senegal, height = 26 mm (from Adam and Knudsen, 1984, pl. 5, fig. 8). Note axial sculpture on early teleoconch whorls (see also Pl. 6, figs. 5–8).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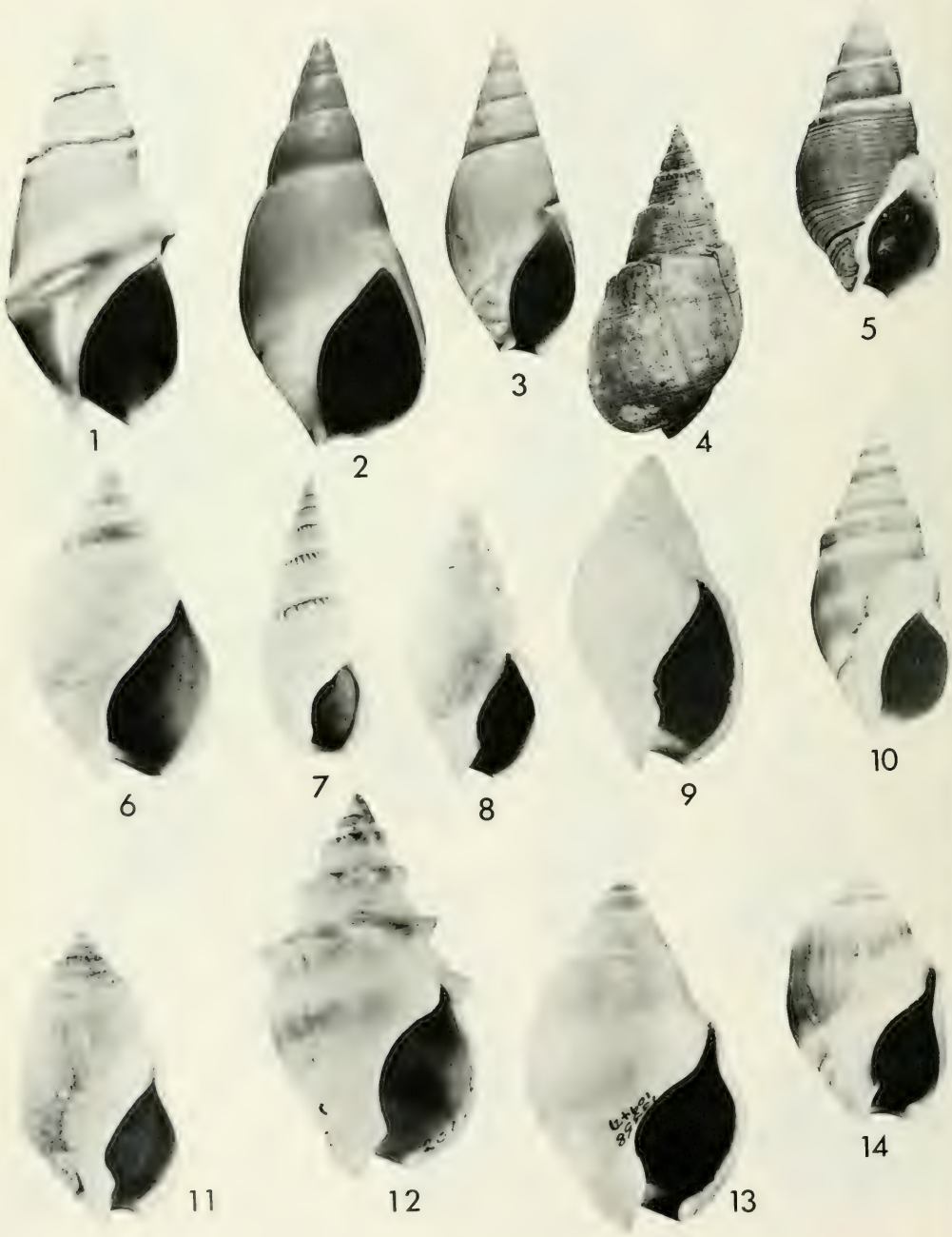
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EXPLANATION OF PLATE 2

Recent species of *Bullia* (*Bullia*) from South Africa and Recent species of *Bullia* (*Buccinanops*) from South America

Figure — Page

Species of *Bullia* (*Bullia*) from South Africa

1. *Bullia* (*Bullia*) *callosa* (Wood, 1828) 13
MCZ(M) 209253, Pt. Alfred, South Africa, height = 46 mm (same specimen as that shown on Pl. 5, figs. 3, 4). Non-surfing species (see p. 13). Type species of the genus *Bullia* Gray, 1834.
2. *Bullia* (*Bullia*) *tenuis* Reeve, 1846 13
MCZ(M) 175842, Jeffrey's Bay, South Africa, height = 56 mm. Non-surfing species.
3. *Bullia* (*Bullia*) *rhodostoma* Reeve, 1847 13
MCZ(M) 93731, Jeffrey's Bay, South Africa, height = 28 mm. Surfing species.
4. *Bullia magna* Haughton, 1932 (? = *Bullia annulata*) 13
Mio-Pliocene, South Africa, height ~ 45 mm (from Haughton, 1932).
5. *Bullia* (*Bullia*) *annulata* (Lamarck, 1816a) 13
MCZ(M) 209245, Pt. Alfred, South Africa, height = 39 mm. Non-surfing species.
6. *Bullia* (*Bullia*) *laevissima* (Gmelin, 1791) 13
(MCZ(M) 209252, Pt. Alfred, South Africa, height = 39 mm.
7. *Bullia* (*Bullia*) *vittata* (Linnaeus, 1767) 13
MCZ(M) 296222, Jeffrey's Bay, South Africa, height = 47 mm.
10. *Bullia* (*Bullia*) *trifasciata* Smith, 1904 20
Topotype, MCZ(M) 101422, Pt. Alfred, South Africa, height = 35 mm.

Species of *Bullia* (*Buccinanops*) from South America

8. *Bullia* (*Buccinanops*) *uruguayensis* Pilsbry, 1897b 26
MCZ(M) 225885, La Paloma, Rocha, Uruguay, height = 24 mm.
9. *Bullia* (*Buccinanops*) *paytensis* (Kiener, 1834) 25
MCZ(M) 296199, Paraca Bay, Peru, height = 48 mm.
11. *Bullia* (*Buccinanops*) *duartei* (Klappenbach, 1961) 27
MCZ(M) 225878, La Coronilla, Uruguay, height = 31 mm.
12. *Bullia* (*Buccinanops*) *monilifera* (Kiener, 1834) 25
MCZ(M) 201351, Punta del Este, Uruguay, height = 54 mm.
13. *Bullia* (*Buccinanops*) *deforme* (King and Broderip, 1831) 26
MCZ(M) 109427, Pt. San Antonio, Argentina, height = 65 mm.
14. *Bullia* (*Buccinanops*) *globulosa* (Kiener, 1834) 20
MCZ(M) 225878, Pt. San Antonio, Argentina, height = 26 mm.

EXPLANATION OF PLATE 3

Specimens of *Bullia* (*Buccinanops*) *cochlidia* (Dillwyn, 1817) from South America, showing range of morphological variation ..... page 20

Figure

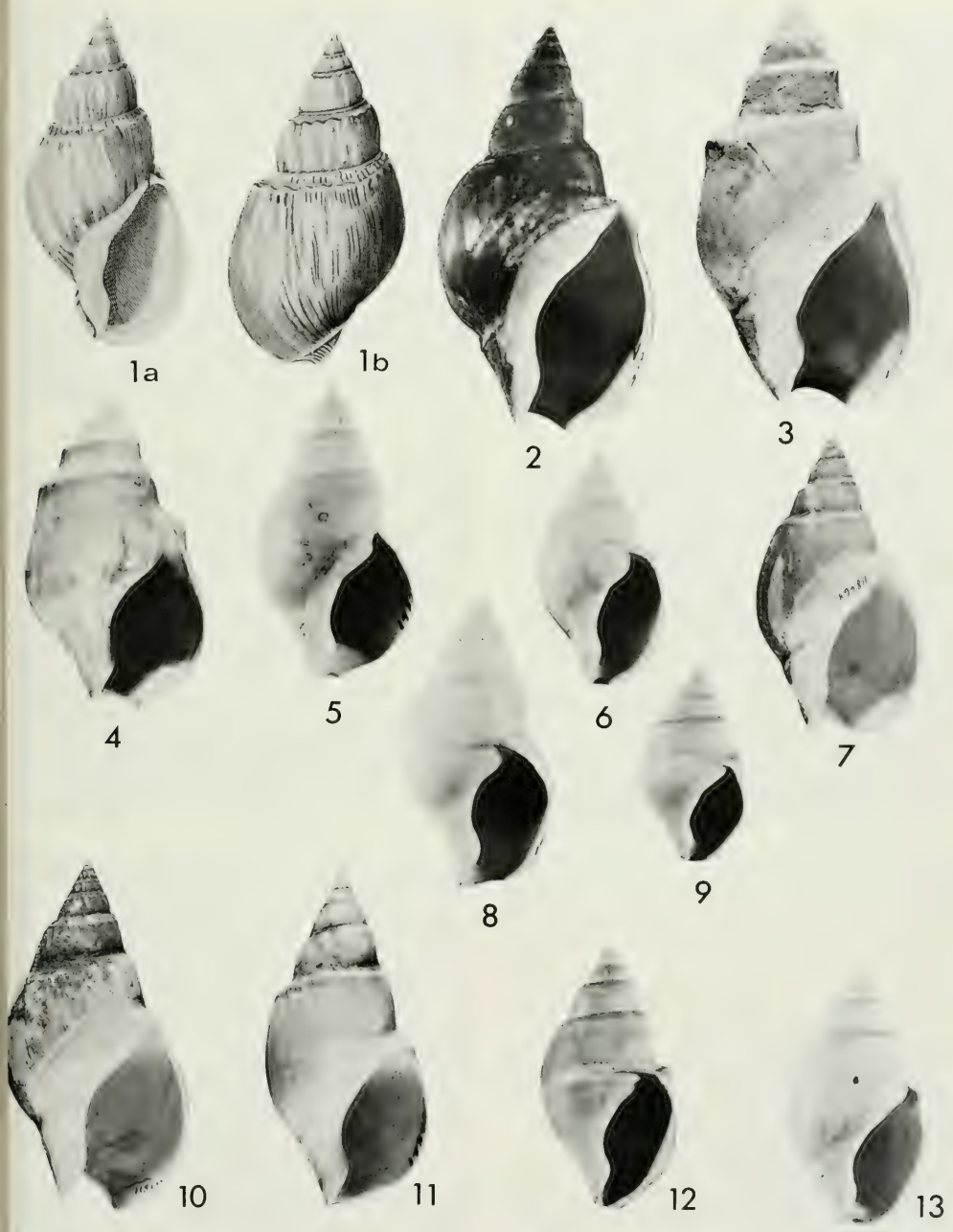
1a, b. *Buccinum Cochlidium* Chemnitz. (from Martini and Chemnitz, 1795, figs. 2053, 2054).

2–13. *Bullia* (*Buccinanops*) *cochlidia* (Dillwyn, 1817).

2. MCZ(M) 219076, Punta del Este, Uruguay, height = 65.0 mm. Specimen showing smooth "*cochlidia*" form.

3. MCZ(M) 198446, Mar de Ajo, Buenos Aires, Argentina, height = 80.0 mm. Specimen showing shouldered "*gradata*" form.

4–13. Specimens more or less intermediate between the extreme *cochlidia* and *gradata* forms. 4, MCZ(M) 296187, Patagonia, height = 59.9 mm; 5, MCZ(M) 198294, Puerto Lobos, Patagonia, height = 57.1 mm; 6, MCZ(M) 296184, no locality data available, height = 47.9 mm; 7, MCZ(M) 118668, Porto Quequen, Buenos Aires, Argentina, height = 63.0 mm; 8, MCZ(M) 198294, Puerto Lobos, Patagonia, height = 55.0 mm; 9, MCZ(M) 296184, no locality data available, height = 40.6 mm; 10, MCZ(M) 118668, Porto Quequen, Buenos Aires, Argentina, height = 74.4 mm; 11, MCZ(M) 198430, San Antonio, Río Negro, Patagonia, height = 54.3 mm; 12, MCZ(M) 296184, no locality data available, height = 54.2 mm; 13, MCZ(M) 219076, Punta del Este, Uruguay, height = 50.8 mm.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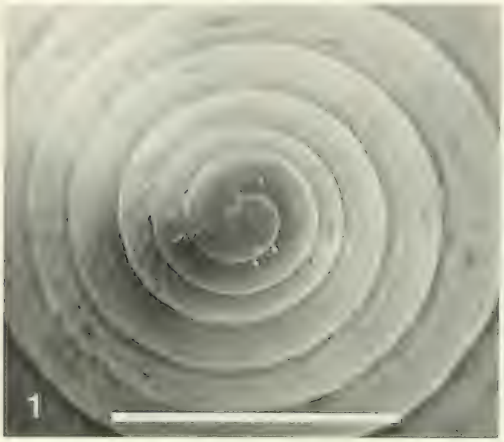
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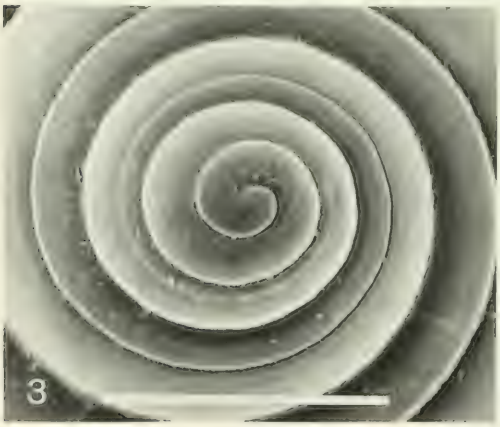
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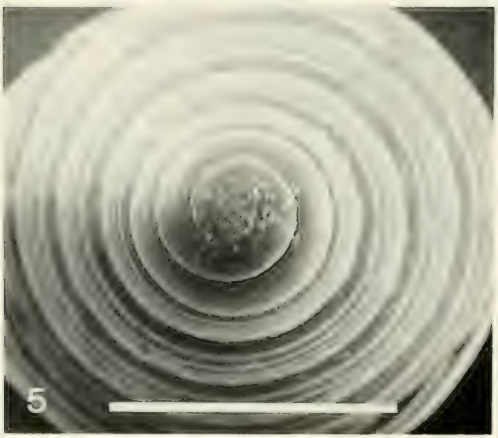
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Explanation of Plate 4

Scanning electron micrographs of shell apices of some Recent species of *Bullia* (*Bullia*) from South Africa
(All scale bars = 1 mm)

Figure — Page

1, 2. *Bullia digitalis* (Dillwyn, 1817) 18
MCZ(M) 29214, juvenile specimen, Walker Bay, South Africa, height = 11.00 mm.
1. apical view (×50).
2. side view (×40).

3, 4. *Bullia laevissima* (Gmelin, 1791) 18
MCZ(M) 296216, juvenile specimen, Saldanha, South Africa, height = 8.0 mm.
3. apical view (×50).
4. side view (×40).

5, 6. *Bullia rhodostoma* ? Reeve, 1847 18
MCZ(M) 296217, juvenile specimen, Jeffrey's Bay, South Africa, height = 5 mm.
5. apical view (×50).
6. side view (×40).

EXPLANATION OF PLATE 5

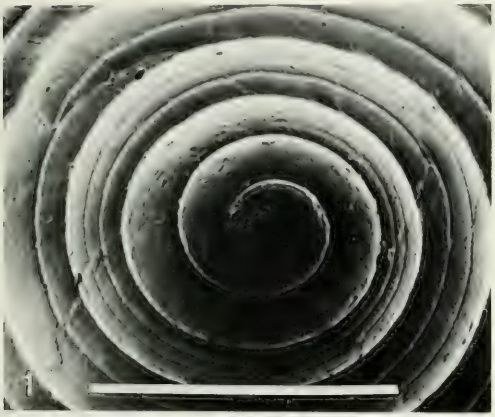
Scanning electron micrographs of shell apices
of some Recent species of *Bullia* (*Bullia*) from South Africa
(All scale bars = 1 mm)

Figure — Page

1, 2. *Bullia annulata* (Lamarck, 1816a) — 13
Adult specimen, MCZ(M) 175864, Jeffrey's Bay, South Africa, height = 27 mm.
1. apical view (×50)
2. side view (×40).

3, 4. *Bullia callosa* (Wood, 1828) — 18
Adult specimen, MCZ(M) 209253, Pt. Alfred, South Africa, height = 42 mm.
3. apical view (×50).
4. side view (×40).

5, 6. *Bullia tenuis* (Reeve, 1846) — 18
Juvenile specimen, MCZ(M) 296215, Pt. Alfred, South Africa, height = 7.0 mm.
5. apical view (×50).
6. side view (×40).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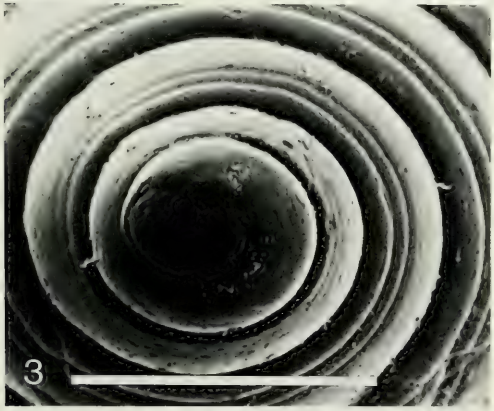
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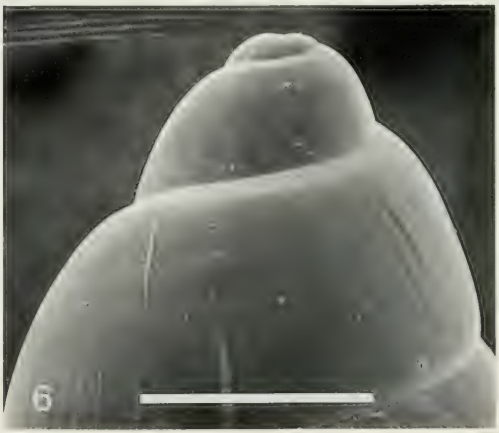
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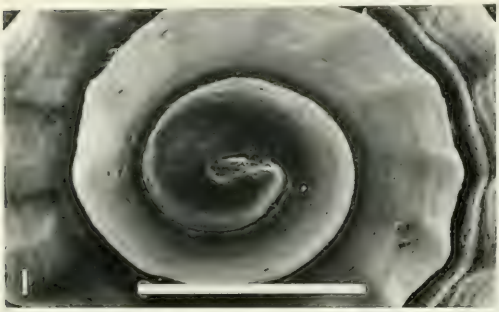
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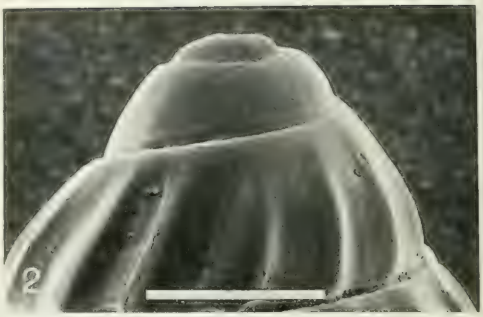
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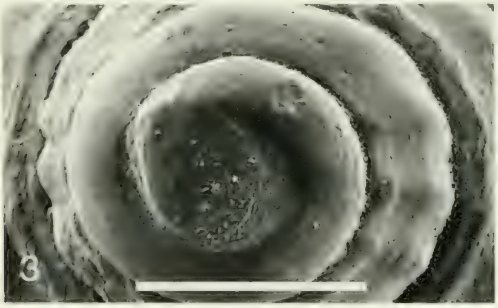
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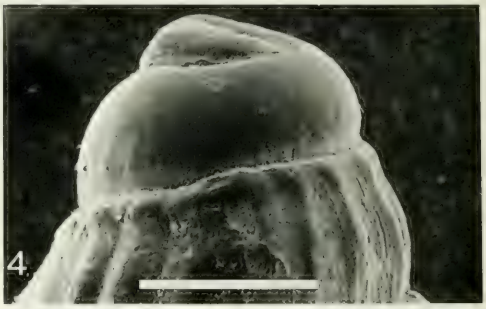
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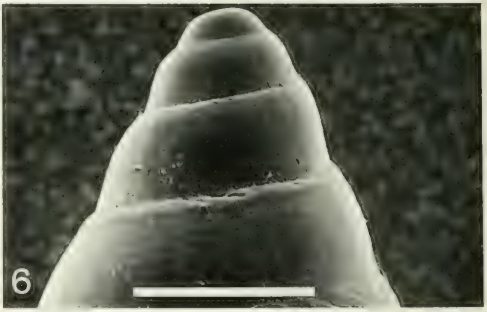
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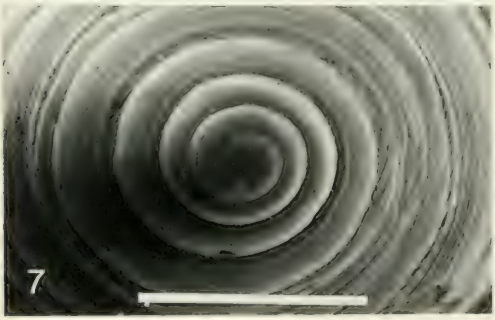
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EXPLANATION OF PLATE 6

Scanning electron micrographs of shell apices of some Recent species of *Bullia* (*Buccinanops*) from South America and *Dorsanum miran* from West Africa

Figure — Page

1–4. Scanning electron micrographs of shell apices of species of *Bullia* (*Buccinanops*) from South America. All scale bars = 1 mm.

1, 2. *Bullia* (*Buccinanops*) *monilifera* (Kiener, 1834) 25
Young specimen, MCZ(M) 296209, height = 22 mm, Brazil. 1, apical view (×50); 2, side view (×40)

3, 4. *Bullia* (*Buccinanops*) *cochlidia* (Dillwyn, 1817) 20
Adult specimen, MCZ(M) 118668, height = 50 mm, Buenos Aires, Argentina. 3, apical view (×50); 4, side view (×40).

5–8. *Dorsanum miran* (Bruguière, 1789) 85
Scanning electron micrographs of shell apices of specimens from West Africa. All scale bars = 1 mm.

5. Apical view of adult specimen, MCZ(M) 29622, height = 25 mm.
6. Side view of adult specimen, MCZ(M) 201967, Senegal, height = 24 mm.
7. Apical view of adult specimen, MCZ(M) 133727, Gambia, height = 27 mm.
8. Apical view of specimen [MCZ(M) 201967] shown in Plate 6, figure 6.

EXPLANATION OF PLATE 7

Fossil species of *Bullia* (*Bulliopsis*)

Figure — Page

1. *Bullia* (*Bulliopsis*) *marylandica* Conrad, 1862a 51
Lectotype (USNM 353125), St. Mary's Fm., Calvert Co., Maryland, height = 29.0 mm.

2. *Bullia* (*Bulliopsis*) *integra* (Conrad, 1842) 50
Syntype (ANSP 15688), St. Mary's Fm., St. Mary's Co., Maryland, height = 17.5 mm.

3–10. *Bullia* (*Bulliopsis*) *quadrata* (Conrad, 1830) 51

3, 4. Syntypes (ANSP 15686) of *Bullia* (*Bulliopsis*) *quadrata* s. s., St. Mary's Fm., St. Mary's Co., Maryland, height = 25.0 mm (fig. 3), 26.0 mm (fig. 4).

5. Hypotype of *Bullia* (*Bulliopsis*) *quadrata* s. s. of Martin, 1904 (USNM 353124), St. Mary's Fm., St. Mary's Co., Maryland, height = 21.0 mm.

6–10. Syntypes (ANSP 15687) of *Bullia* (*Bulliopsis*) *subcylindrica* (Conrad, 1862a)
Syntypes (ANSP 15687), St. Mary's Fm., St. Mary's Co., Maryland, height = 27.5 mm (fig. 6).

11, 12. *Bullia* (*Bulliopsis*) *quadrata bowlerensis*, new subspecies 52
Cobham Bay Member, Eastover Fm., Bowler's Wharf, Essex Co., Virginia.

11. Holotype, MCZ(IP) 29208, height = 29.6 mm.

12. Paratype, MCZ(IP) 29209, height = 25.5 mm.

13–17. *Bullia* (*Bulliopsis*) *choctavensis* (Aldrich, 1886) 53

13a, b. Holotype of *Nassa calli* Aldrich, 1886, USNM 638770, Lisbon Formation, Lisbon Bluff, Alabama River, Monroe Co., Alabama, height = 30.0 mm.

14. Holotype, USNM 638787, Hatchetigbee Formation, Hatchetigbee Bluff, Tombigbee River, Washington Co., Alabama, height = 11.9 mm.

15, 16. Topotypes, MCZ(IP) 29192, Hatchetigbee Formation, Hatchetigbee Bluff, Tombigbee River, Washington Co., Alabama, height = 10.2 mm (fig. 15), 10.1 mm (fig. 16).

17a, b. MCZ(IP) 29254, Nanafalia Formation, Dale Co., Alabama, height = 15.0 mm.

18–22. *Bullia* (*Bulliopsis*) *variabilis* (Whitfield, 1894) 52
Kirkwood Formation, Cape May, New Jersey.

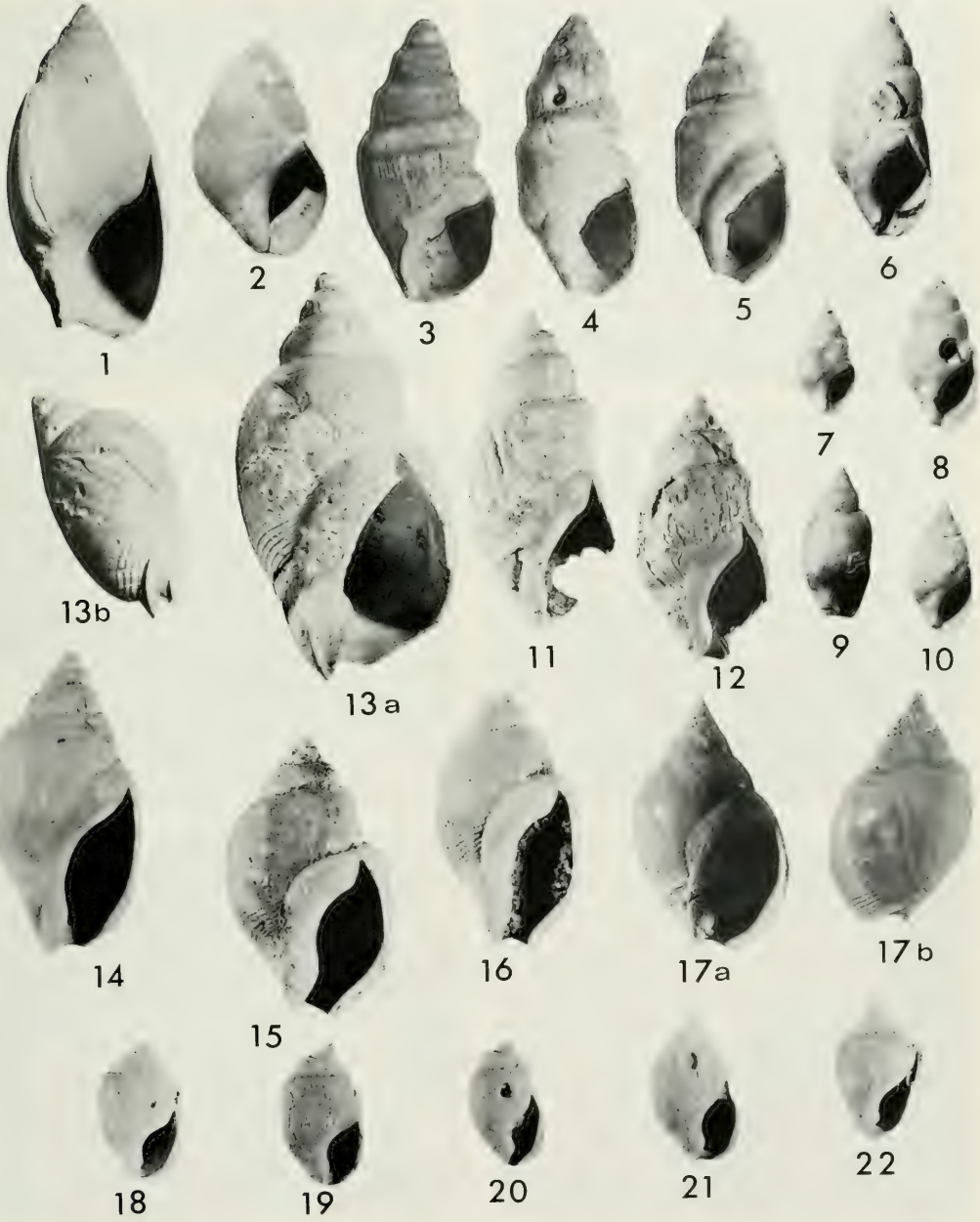
18. Syntype, ANSP 10409, height = 9.0 mm.

19. ANSP 15685, height = 9.0 mm.

20. ANSP 15685, height = 8.3 mm.

21. ANSP 14478, height = 9.8 mm.

22. ANSP 15685, height = 9.0 mm.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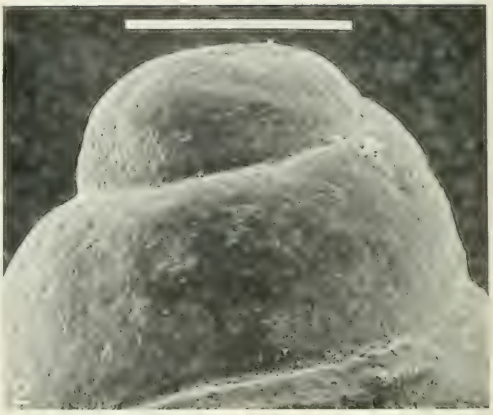
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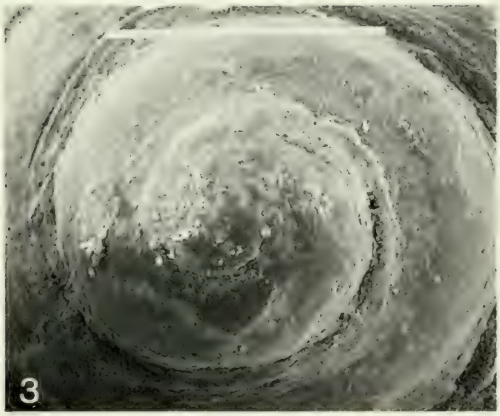
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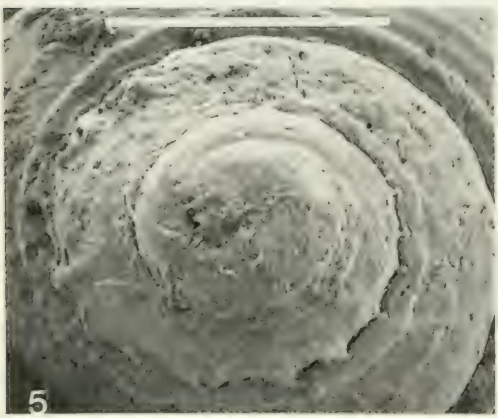
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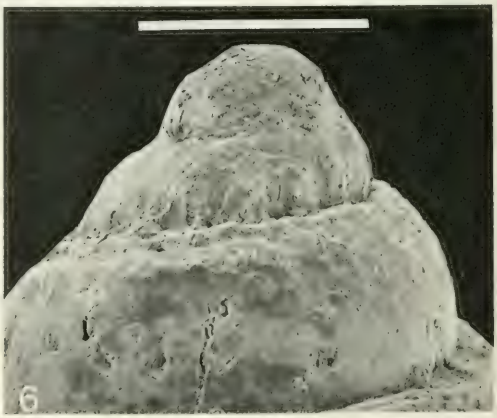
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EXPLANATION OF PLATE 8

Scanning electron micrographs of shell apices
of specimens of *Bullia* (*Bulliopsis*) from the Miocene of Maryland and Virginia,
and the Eocene of Alabama
(All scale bars = 1 mm)

Figure

1, 2. *Bullia* (*Bulliopsis*) *marylandica* Conrad, 1862a ..... Page 51
MCZ(IP) 29195, Little Cove Point, Calvert Co., Maryland, height = 21 mm.
1. apical view (×50).
2. side view (×40).

3, 4. *Bullia* (*Bulliopsis*) *quadrata bowlerensis*, new subspecies 52
MCZ(IP) 29193, Bowlers Wharf, Essex Co., Virginia, height = 23 mm.
3. apical view (×50).
4. side view (×40).

5, 6. *Bullia* (*Bulliopsis*) *choctavensis* (Aldrich, 1886) 53
MCZ(IP) 29191, Hatchetigbee Bluff, Tombigbee River, Alabama, height = 9 mm.
5. apical view (×50).
6. side view (×40).

EXPLANATION OF PLATE 9

Fossil species from the U. S. Gulf Coast previously allied with the *Bullia* group

Figure — Page

1, 3. "*Bullia*" *tenera* (Conrad, 1834) — 58
Lisbon Fm., Claiborne, Monroe Co., Alabama.
1. Hypotype (PRI 3066), height = 37.5 mm.
3. Hypotype (PRI 3064), height = 22 mm.

2. "*Bullia*" *scamba* (Conrad, 1832b) — 58
Hypotype (PRI 3082), Gosport Sand, Claiborne, Monroe Co., Alabama, height = 32.0 mm.

4. "*Bullia* (*Anbullina*)" *ancillops* (Heilprin, 1891) — 59
Hypotype (PRI 3045), Lisbon Fm., Claiborne, Monroe Co., Alabama, height = 25 mm.

5. *Bulovia weisbordi* Palmer, 1937 — 60
Holotype (PRI 3048), Weches Fm., Smithville, Bastrop Co., Texas, height = 19 mm.

6. "*Dorsanum*" *scalatum* (Heilprin, 1891) — 62
Hypotype (PRI 3051), Weches Fm., Smithville, Bastrop Co., Texas, height = 16.3 mm.

7. "*Dorsanum*" *bellaliratum* (Gabb, 1862) — 61
Probably the holotype (ANSP 17110), Gosport Sand, Claiborne, Alabama, height = 18 mm.

8. "*Buccinanops*" *ellipticum* (Whitfield, 1865) — 59
Hypotype (LSU 6023), Pendleton Fm., Pendleton Bluff, Sabine River, Sabine Co., Texas, height = 28.3 mm.

9. *Monoptygma leai* Whitfield, 1865 — 60
Syntype (FMNH-UC 24671), Lisbon Fm., Lisbon Bluff, Alabama River, Monroe Co., Alabama, height = 23.3 mm.

10. "*Bullia*" *altilis* (Conrad, 1832b) — 56
Hypotype (PRI 3044) of "*Bullia*" *altilis subglobosa* (Conrad, 1832b), Bashi Fm., Hatchetigbee Bluff, Tombigbee River, Washington Co., Alabama, height = 22.5 mm.

11. *Bullia calluspira* Dockery, 1980 — 57
Holotype (PRI 30022), Bashi Fm., Meridian, Lauderdale Co., Mississippi, height = 28 mm.

12. "*Ancillopsis*" *patula* (Deshayes, 1835) — 86
Ducy, near Montepilloy, France, upper Eocene (Bartonian) (specimen from collection of L. Dolin, St. Denis, France), height = 30.2 mm.

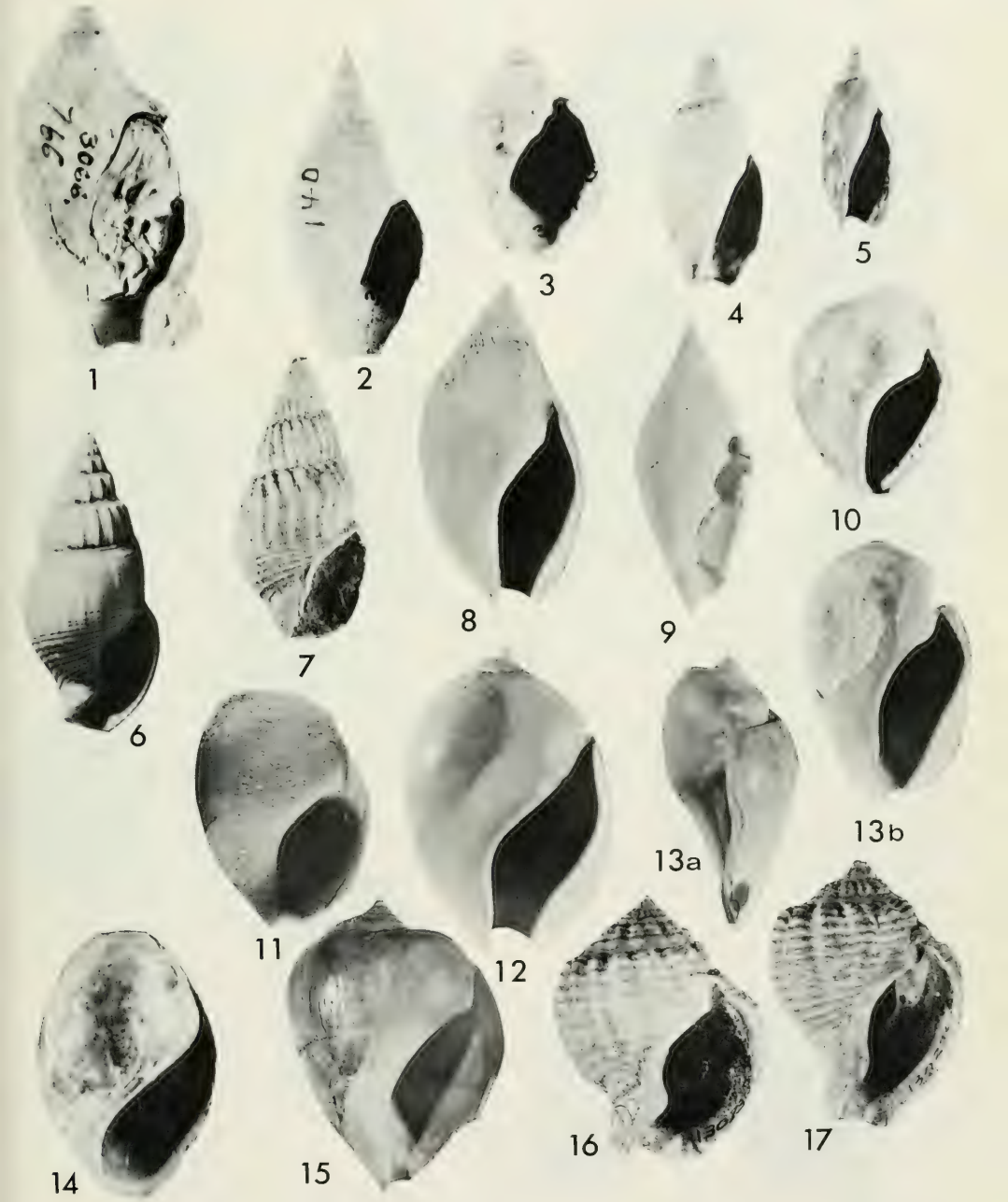
13a, b. "*Bullia*" *tuomeyi* (Aldrich, 1921) — 59
Holotype (GSATC 39), Bell's Landing Mbr., Tuscahoma Fm., Bell's Landing, Alabama River, Monroe Co., Alabama, height = 28 mm.

14. "*Melanopsis*" *anita* (Aldrich, 1886) — 63
Holotype (USNM 638788), Gregg's Landing Mbr., Tuscahoma Fm., Gregg's Landing, Alabama River, Monroe Co., Alabama, height = 7.1 mm.

15. *Pseudoliva vetusta* (Conrad, 1833b) — 63
MCZ(IP) 29253, Hatchetigbee Fm., Hatchetigbee Bluff, Tombigbee River, Washington Co., Alabama, height = 37.1 mm.

16. *Buccinopsis crassa* (Wade, 1917) — 53
Topotype (USNM 130234), Upper Cretaceous, Ripley Formation, McNairy Co., Tennessee, height = 40.6 mm.

17. *Buccinopsis solida solida* (Wade, 1917) — 53
USNM 130235, Upper Cretaceous, Ripley Fm., Union Co., Mississippi, height = 40.5 mm.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EXPLANATION OF PLATE 10

Fossil species from the west coast of North America previously allied with the *Bullia* group

Figure — Page

1a, b, 4. "*Molopophorus*" *anglonanus* (Anderson, 1905) 64
1a, b. Neotype (CAS 91), Monterey Shale, Kern Co., California, height = 35 mm. Note recurved siphonal channel around fasciole in figure 1b.
4. Hypotype (UCMP 32018), Kern Co., California height = 17.3 mm.

2, 3. "*Molopophorus*" *dalli* Anderson and Martin, 1914 66
2. Holotype (CAS 168), San Emigdio Fm., Kern Co., California, height = 30 mm.
3. Paratype (CAS 169), San Emigdio Fm., Kern Co., California, height = 20 mm.

5. "*Molopophorus*" *lincolnensis* Weaver, 1916 66
Unnumbered specimen from UCMP loc. A-9, Lincoln Creek Fm., Thurston Co., Washington, height = 21.1 mm.

6. "*Molopophorus*" *biplicatus* (Gabb, 1866) 66
MCZ(IP) 27846, horizon unknown, Contra Costa Co., California, = 47 mm.

7. "*Molopophorus*" *matthewi* Etherington, 1931 65
Holotype (UCMP 32038), Astoria Fm., Grays Harbor Co., Washington, height = 47 mm.

8–10. *Colwellia antiquata* (Gabb, 1864) 70
8. Hypotype (UCMP 30750), Kings Co., California, height = 5.5 mm.
9. Hypotype (UCMP 15939), Kings Co., California, height = 7.0 mm.
10. Hypotype (UCMP 33246), Kings Co., California, height = 19.0 mm.

11. "*Molopophorus*" *clarki* (Weaver, 1912) 67
Holotype (CAS 494), Cowlitz Fm., Cowlitz Valley, Washington, height = 32 mm.

12. *Bullia* (*Buccinanops*) ? *clarki* Wagner and Schilling, 1923 70
Holotype (UCMP 11430), San Emigdio Fm., Kern Co., California, height = 38 mm.

13. *Colwellia tejonensis* (Dickerson, 1915) 69
Unnumbered specimen from UCMP loc. A-858, Coaledo Fm., Coos Co., Oregon, height = 23.3 mm.

14. *Brachysphingus* species 64
Unnumbered specimen from UCMP loc. A-1620, Martinez Fm., Contra Costa Co., California, height = 30.0 mm.

15. "*Molopophorus*" *fishii* (Gabb, 1869) 68
Syntype of *Bullia buccinoides* Merriam, 1899 (UCMP 11929), Sooke Fm., Vancouver Island, British Columbia, Canada, height = 30 mm.

EXPLANATION OF PLATE 11

Fossil species assignable to the genus *Calophos* Woodring, 1964

Figure — Page

1, 2. *Calophos ectyphus* Woodring, 1964 — 73
1. Holotype (USNM 643659), Gatun Fm., former Canal Zone, Panama, height = 40.7 mm. Axially sculptured form.
2. Hypotype (USNM 643658), Gatun Fm., former Canal Zone, Panama, height = 39 mm. Smooth form.

3. *Calophos inornatus* (Gabb, 1881) — 74
Syntype (ANSP 3483), Costa Rica, height = 34 mm.

4, 5. *Calophos* species — 72
Eocene, Tonosí area, Panama, USGS loc. 8426.
4. USNM 434948, height ~ 30 mm.
5. USNM 434949, height ~ 30 mm.

6. *Calophos bombax* (Olsson, 1964) — 74
Holotype (USNM 644013), Borbon Fm., Ecuador, height = 43.6 mm.

7. *Calophos ursus* (Olsson, 1964) — 74
Holotype (USNM 644041), Angostura Fm., Ecuador, height = 37.5 mm.

8. *Calophos rohri* (Rutsch, 1942) — 76
Holotype (NHMB H6187), Springvale Fm., Trinidad, height = 37.6 mm.

9. *Calophos* species of Woodring (1964) — 72
USGS loc. 8345, Boca del Toro, Panama, height = 40.0 mm. Woodring (1964, p. 262) suggested that this specimen belongs to an undescribed species (see Table 9).

10. *Calophos oldroydae* (Dall and Ochsner, 1928) — 77
Holotype (CAS 2926), Isla Baltra, Galapagos Islands, height = 55 mm.

11. *Calophos tropicalis* (Dall and Ochsner, 1928) — 77
Holotype (CAS 2925), Isla Baltra, Galapagos Islands, height = 65 mm.

12. *Calophos* species of Woodring (1964) — 72
USNM 644382 Boca del Toro, Panama, height = 39.0 mm. This may be the same species as that shown in Plate 11, figure 9.

13. *Calophos golfoyaquensis* (Maury, 1917) — 77
Syntype (PRI 28741), Cercado de Mao, Dominican Republic, height = 14.5 mm.

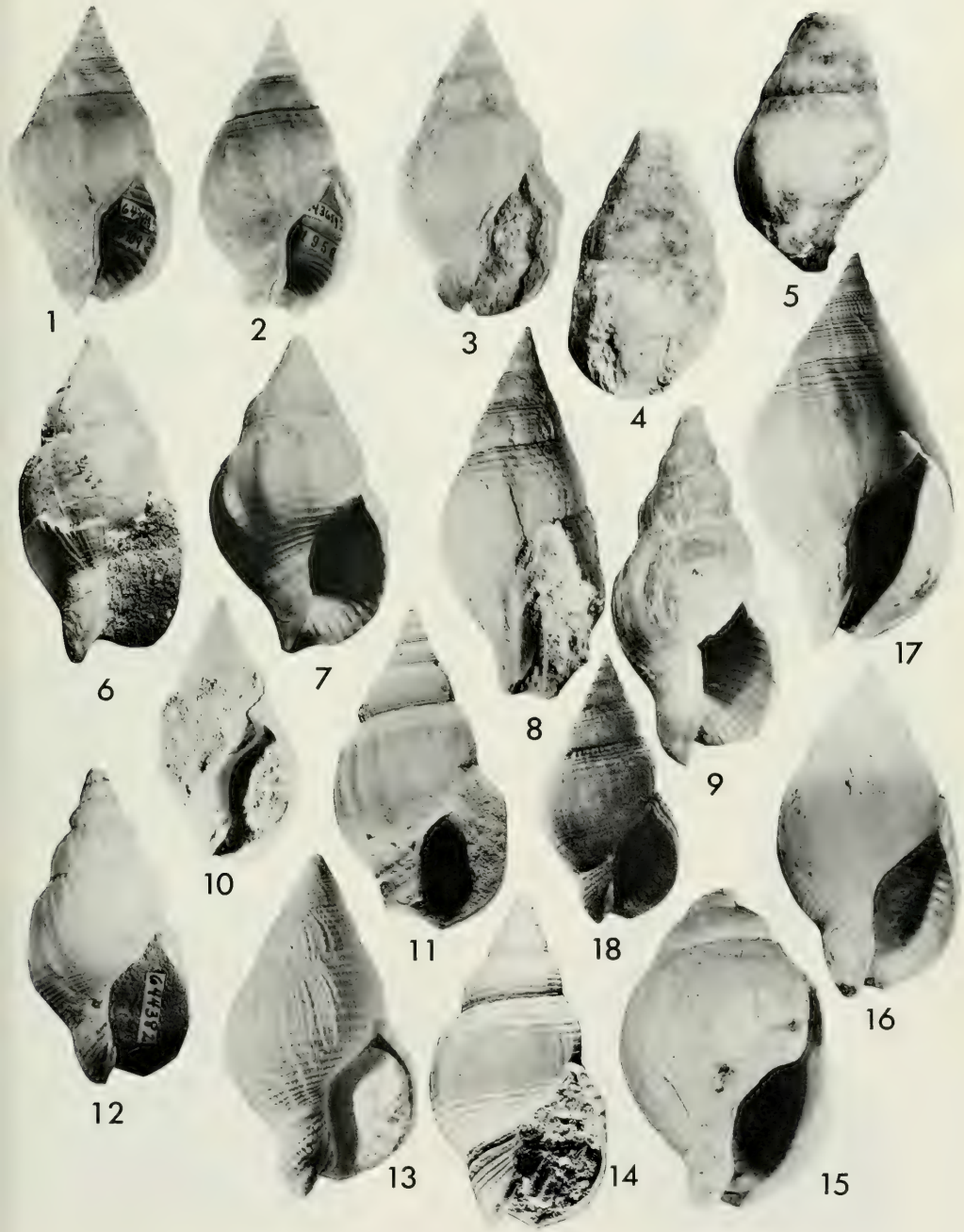
14. *Calophos wilsoni*, new species — 75
Holotype MCZ(IP) 29351, APAC pit, Sarasota Co., Florida, "Pinecrest Formation", height 39.0 mm.

15. *Calophos* (?) *esmereldensis* (Olsson, 1964) — 76
Holotype (USNM 644203), Esmeraldas Fm., Ecuador, height = 46.5 mm.

16. *Calophos baranoanus* (Anderson, 1929) — 76
Hypotype (USNM 347228), Cubagua Island, Venezuela, height = 58.9 mm.

17. *Calophos rohri* (Rutsch, 1942) — 76
Hypotype (NHMB H15216), Springvale Fm., Trinidad, height = 42.9 mm.

18. *Calophos mixteca* (Perrilliat Montoya, 1963) — 77
Holotype G-IGM 1112, Agueguexquite Fm., Tehuantepec, Mexico (from Perrilliat Montoya, 1963, pl. 4, figs. 16, 17), height ~ 36 mm.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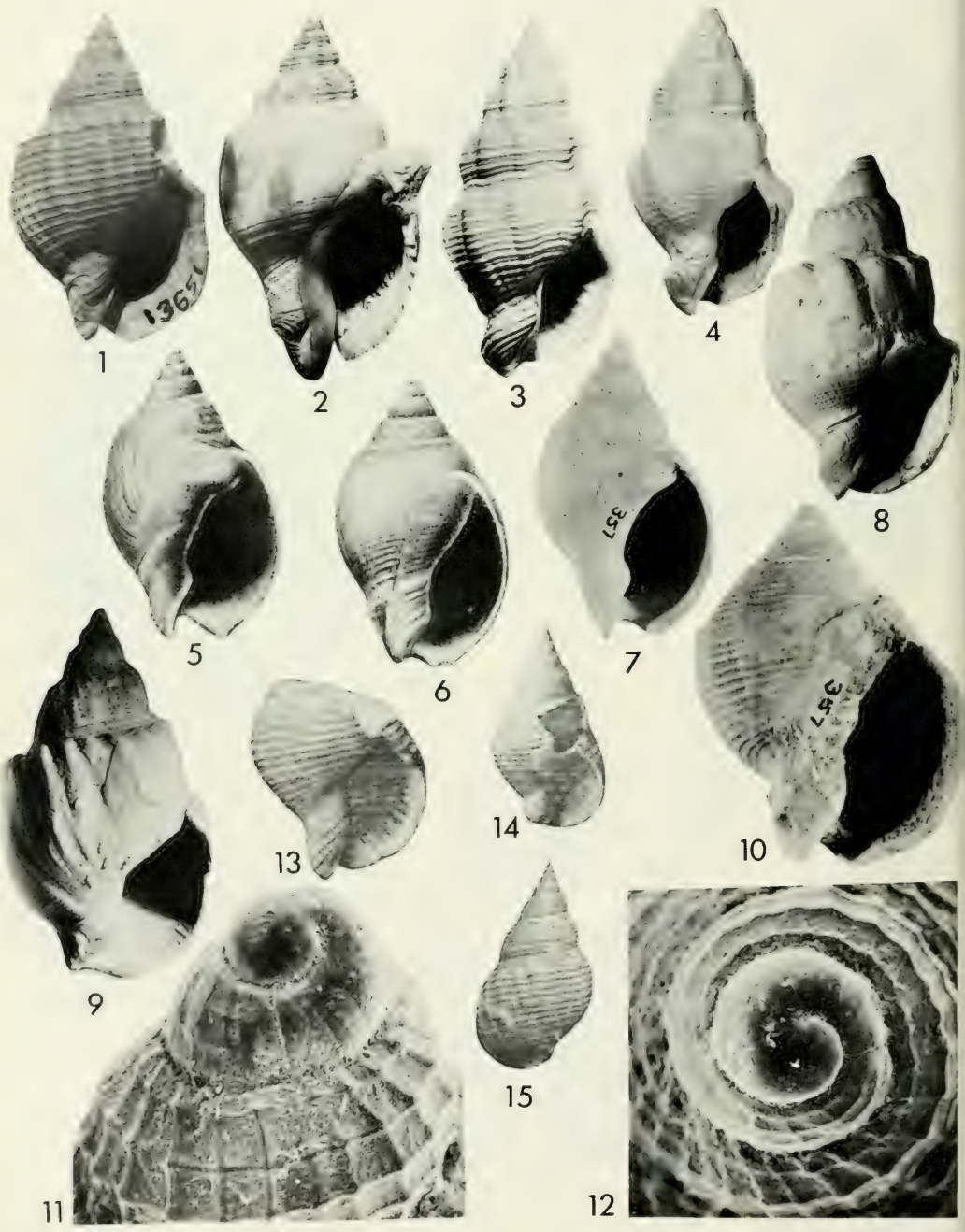
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EXPLANATION OF PLATE 12

Miscellaneous fossil species from North, Central, and South America allied to the *Bullia* group

Figure — Page

1. "*Perunassa*" *ecuadorensis* (Pilsbry and Olsson, 1941) 79
   Syntype (ANSP 13651), Canoa Fm., Punta Blanca, Ecuador, height = 39.0 mm.
2. *Northia* (*Nicema*) *noctua* Olsson, 1964 72
   Holotype (USNM 644018), Angostura Fm., Telembi, Río Cayapas, Ecuador, height = 42.7 mm.
3. *Cymatophos veatchi* (Olsson, 1922) 72
   USNM 643653, Gatun Fm., Costa Rica, height = 44.1 mm.
4. *Phos tuberaensis* Anderson, 1929 72
   USGS loc. 24702, Cantaure, Venezuela, height = 41.0 mm.
5. *Bullia* (*Buccinanops*) *nordenskjoldi* (Steinmann and Wilckens, 1908) 80
   Lower Miocene, Tierra del Fuego, height ~ 90 mm. (from Steinmann and Wilckens, 1908, pl. 7, fig. 2).
6, 7. *Bullia* (*Buccinanops*) *fuegina* (Steinmann and Wilckens, 1908) 80
   6. Lower Miocene, Tierra del Fuego, height ~ 38 mm. (from Steinmann and Wilckens, 1908, pl. 7, fig. 1).
   7. MCZ(IP) 29289, Isla Grande, Tierra del Fuego, height = 38.9 mm.
8, 9. *Calophos* ? *zorritensis* (Nelson, 1870) 78
   8. Syntype (YPM 598), Tumbez Fm., Peru, height = 48.8 mm.
   9. Syntype (YPM 504), Tumbez Fm., Peru, height = 41.0 mm.
10. *Austrocominella fuegensis* (Ihering, 1907) 81
    MCZ(IP) 29190, Carman Silva, Isla Grande, Tierra del Fuego, height = 40.1 mm.
11, 12. *Calophos wilsoni*, new species 75
    USNM 434950, Acline, Charlotte Co., Florida, "Pinecrest Formation".
    11. Lateral view, ×50.
    12. Apical view, ×50.
13–15. *Calophos plicatilis* (Böse, 1906) 74
    Paso Real near Tuxtepec, Oaxaca, Mexico (from Böse, 1906).
    13. (from Böse, 1906, pl. 4, fig. 22).
    14. (from Böse, 1906, pl. 4, fig. 23) height = 23 mm.
    15. (from Böse, 1906, pl. 4, fig. 24) height = 29.5 mm.

EXPLANATION OF PLATE 13

Fossil species from South America and Europe previously placed in the genus *Dorsanum*

Figure — Page

1a, 1b, 2. "*Dorsanum*" *parinense* (Olsson, 1928) 71

1a, 1b. Paratype (PRI 3667), Parinas Fm., Peru, height = 15 mm. Note recurved siphonal channel around fasciole.

2. Holotype (PRI 3666), Parinas Fm., Peru, height = 17 mm.

3a, 3b, 4. "*Dorsanum*" *lagunitense* (Woods, 1922) 71

3a, b. Restin Fm., Peru (from Woods, 1922, pl. 13, fig. 1).

4. Restin Fm., Peru (from Woods, 1922, pl. 12, fig. 12).

5–7, 10, 11. European representatives of taxa formerly assigned to the genus *Dorsanum*. These specimens are from the old European collections of the MCZ; all appear to be from the Miocene of France, but more precise information is unavailable. Species names given for these specimens are those appearing on the museum labels, and they have not been compared with original figures or descriptions. Specimens in figures 5, 6 and 10, and perhaps 8 and 9 as well, appear to be assignable to the group referred to here as "*Cyllenina*" 1. The specimen in figure 7 bears a recurved siphonal channel and is representative of the group referred to here as "*Cyllenina*" 2, believed to be closely related to *Dorsanum* s. s.

5. *Buccinum duplicatum* Sowerby, 1832 86

MCZ(IP) 6003, height = 18.8 mm.

6, 7. *Buccinum baccatum* Basterot, 1825 85

6. MCZ(IP) 6001, height = 21.4 mm; 7a, 7b. MCZ(IP) 5995, height = 19.2 mm. 7b. Closeup of dorsal anterior region, showing siphonal canal.

10. "*Buccinum burdigalinum*" 86

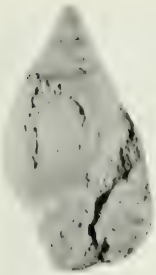
MCZ(IP) 3808, height = 26.2 mm.

11a, b. *Nassa veneris* Faujas de Saint-Fond, 1817 86

MCZ(IP) 6004a, height = 40.0 mm. 11a, ventral (apertural) view; 11b, dorsal view.

8, 9. *Bullia hungarica* (Gábor, 1936) 86

Oligocene, Hungary, height ~ 28 mm (from Baldi, 1973, pl. 38, fig. 15).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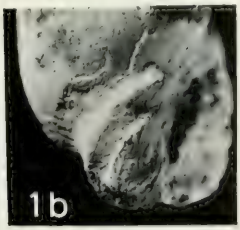
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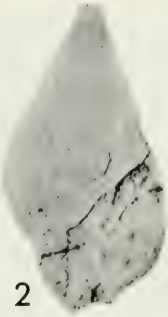
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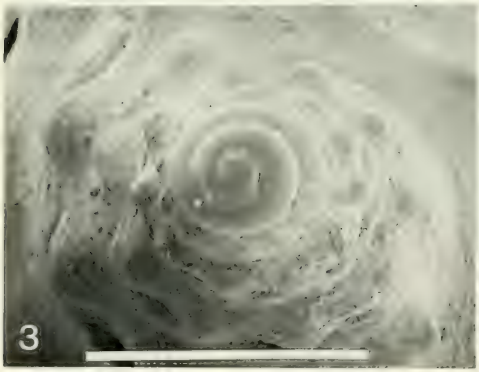
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EXPLANATION OF PLATE 14

Scanning electron micrographs of shell apices of fossil species from the Tertiary of Europe usually assigned to *Dorsanum* ..... page 84

Species names are taken from museum labels, and have not been compared with original figures or descriptions. All scale bars = 1 mm.

Figure — Page

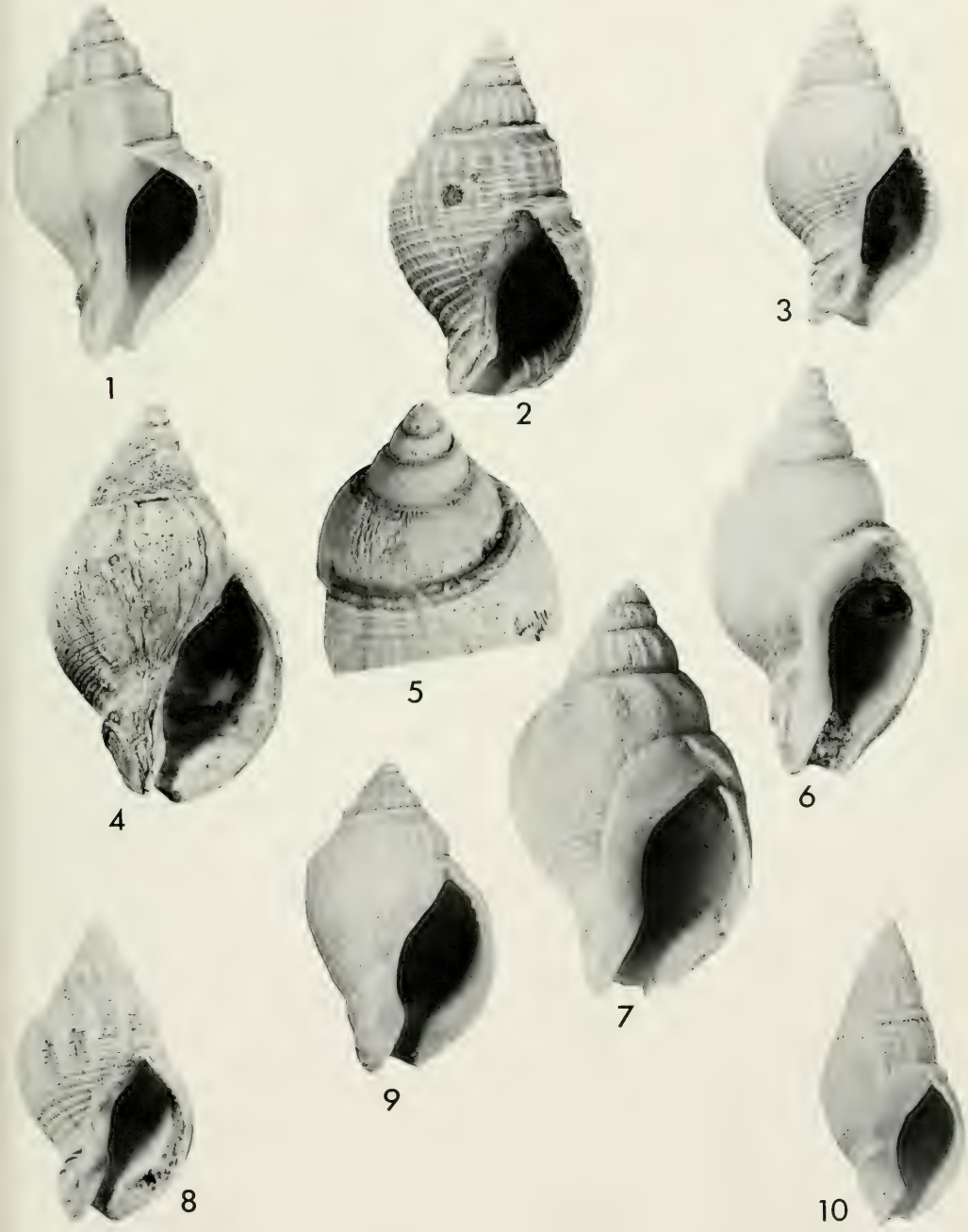
1, 2. "*Buccinum duplicatum*"
   1. MCZ(IP) 6003, apical view (×50).
   2. MCZ(IP) 6003, side view (×40).
3, 4. "*Buccinum baccatum*"
   3. MCZ(IP) 6002, apical view (×50).
   4. MCZ(IP) 6002, side view (×40).
5, 6. "*Dorsanum veneris*"
   5. MCZ(IP) 6004, apical view (×50).
   6. MCZ(IP) 6004, side view (×40).

EXPLANATION OF PLATE 15

Representative species of the fossil genera described by Nuttall and Cooper (1973) from Paleogene strata of western Europe. This plate was composed from original plate photos provided by J. Cooper and C. P. Nuttall of the BM(NH).

Figure — Page

1. *Pseudocominella armata* (Sowerby, 1850) — 82
   BM(NH) GG 19685/3, middle Eocene, Bramshaw, Hampshire, England, height = 16 mm.
2. *Pseudocominella deserta* (Solander, 1766) — 82
   Lectotype (BM(NH) GG 19667), upper Eocene, Barton-on-Sea, Hants, England, height = 26.8 mm.
3. *Pseudocominella solanderi* (Cossmann, 1889) — 82
   Neotype (BM(NH) GG 19693/1), upper Eocene, Hampshire, England, height = 14.7 mm.
4. 5. *Desortinassa desori* (Deshayes, 1865) — 82
   4. BM(NH) GG 19438/1, Jonchery-sur-Vesle, France, height = 17.6 mm.
   5. BM(NH) GG 19438/2, Jonchery-sur-Vesle, France, juvenile specimen (×7).
6. *Whitecliffia suturosa* (Nyst, 1836) — 83
   BM(NH) GG 19720/1, Latdorf, Germany, height = 16.1 mm.
7. *Whitecliffia tumida* Nuttall and Cooper, 1973 — 83
   Holotype (BM(NH) GG 19722/1), upper Eocene, Whitecliff Bay, Isle of Wight, England, height = 12.9 mm.
8. *Keepingia gossardi* (Nyst, 1836) — 83
   BM(NH) GG 19739/1, Etampes, France, height = 23 mm.
9. *Colwellia flexuosa* (Edwards, 1866) — 83
   Lectotype (BM(NH) GG 19709/1), upper Eocene, Colwell Bay, Isle of Wight, England, height = 14.2 mm.
10. *Thanetinassa bicorona* (Melleville, 1843) — 83
    Chalons-sur-Vesle, France, height = 16 mm.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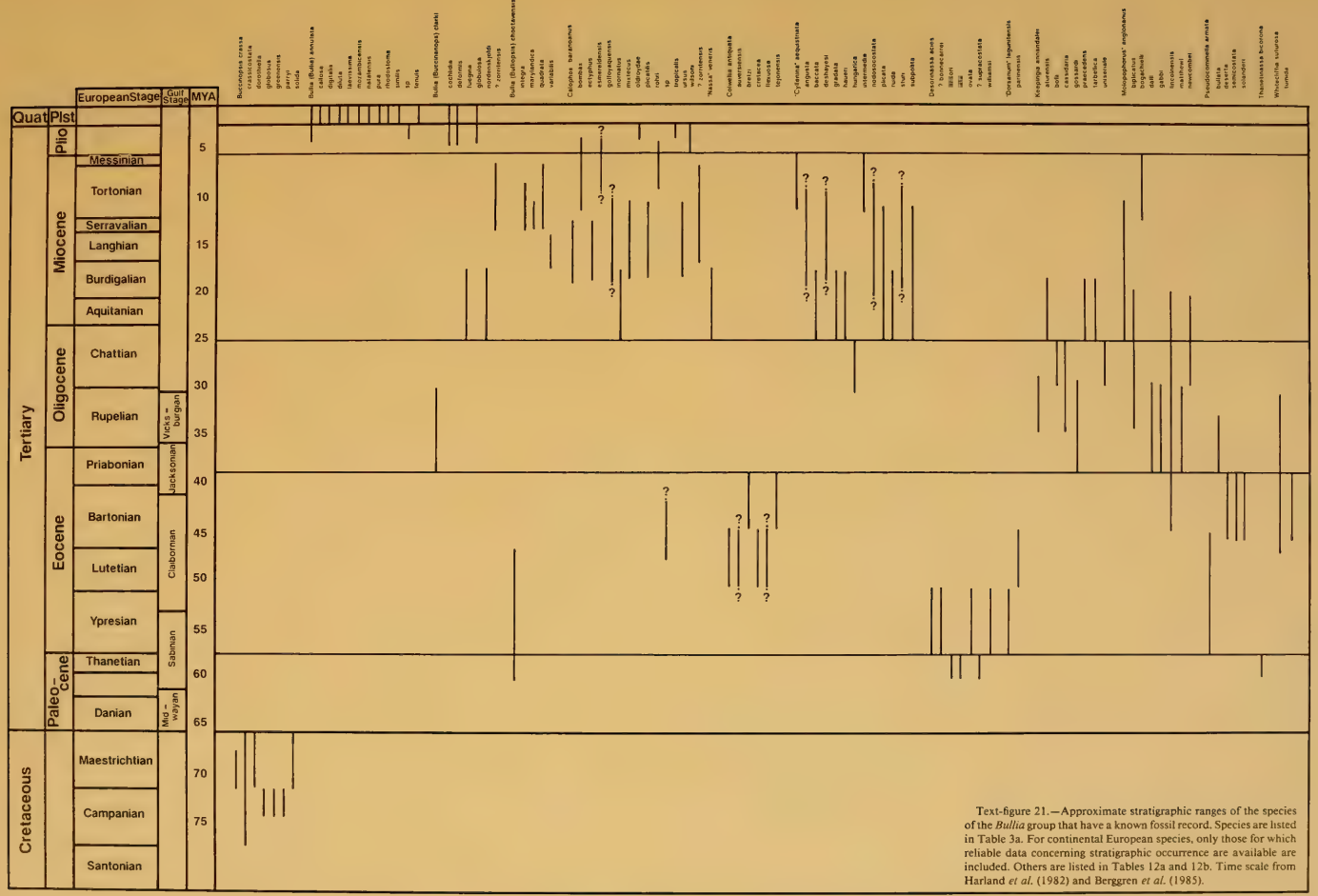

Text-figure 21.—Approximate stratigraphic ranges of the species of the *Bullia* group that have a known fossil record. Species are listed in Table 3a. For continental European species, only those for which reliable data concerning stratigraphic occurrence are available are included. Others are listed in Tables 12a and 12b. Time scale from Harland *et al.* (1982) and Berggren *et al.* (1985).

PREPARATION OF MANUSCRIPTS

Bulletins of American Paleontology usually comprises two or more separate monographs in two volumes each year. This series is a publication outlet for significant longer paleontological monographs for which high quality photographic illustrations and the large quarto format are a requisite.

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Collinson, J.
1962. *Size of lettering for text-figures.* Journal of Paleontology, vol. 36, p. 1402.

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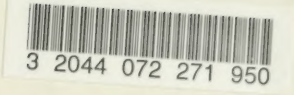
ISBN 0-87710-417-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